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Raymond Gerard Albright
Loyola University Chicago

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THE FUNCTIONAL MORPHOLOGY AND PHYLOGENETIC SIGNIFICANCE OF THE DEGLUTITIONAL MECHANISM IN THE GENERALIZED COLUBRID *ELAPHE OBSOLETA QUADRIVITTATA*

by

Raymond Gerard Albright, S.J.

A Dissertation Submitted to the Faculty of the Graduate School of Loyola University in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

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LIFE

Raymond Gerard Albright, S. J., was born in Detroit, Michigan, April 1, 1926.

He was graduated from the University of Detroit High School in June, 1944, and entered the Society of Jesus the same year. During the following five years he pursued humanistic studies at Milford College of Xavier University, Cincinnati, Ohio, and at West Baden College of Loyola University, Chicago. He was graduated from Loyola with the degree of Bachelor of Arts in June, 1949.

From 1948 to 1951 he was engaged in philosophical studies at West Baden College and at Spring Hill College, Mobile, Alabama. At the latter institution he completed his undergraduate work in the biological sciences. After a summer of study at John Carroll University, Cleveland, Ohio, he was accepted as a candidate for the Master of Science degree in the Department of Anatomy of Loyola University, Chicago, in September of 1951. He received his Master of Science degree in June, 1953.

Work toward the Doctorate degree was begun in the same department during the summer of 1953. Part of the summer of the year 1954 was spent at the Marine Biological Laboratories, Woods Hole, Massachusetts. He was awarded a graduate Research Fellowship by the Standard Oil Company of Indiana in July, 1954.

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During the course of the present investigation the author has received assistance from many sources. He is especially indebted to the following.

Mr. Clifford H. Pope, formerly Curator of Reptiles at the Chicago Natural History Museum, originally suggested the problem and outlined some of the significant contributions such a study would afford.

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Karl P. Schmidt, PhD., Chief Curator of Zoology, and Robert F. Inger, PhD., Curator of Reptiles, have been courteous and obliging in providing the writer with full access to the herpetological collections and other research facilities of the Chicago Natural History Museum, and have likewise assisted him with numerous helpful suggestions concerning various aspects of the work. Through their courtesy, and that of Mr. Hymen Marx, also of the Division of Reptiles, the author received a large collection of unaccessioned lizards and snakes (including a specimen of Varanus salvator) for use in the present anatomical studies. Mr. D. Dwight Davis, Curator of Anatomy, has generously provided access to the extensive osteological collections of the Museum.

To Mr. Marlin Perkins, Director of the Lincoln Park Zoo in Chicago, the author wishes to express his appreciation for allowing him to observe the deglutitional activities of snakes in the Zoo, and for providing several specimens for anatomical study, including a litter of juvenile rattlesnakes, Crotalus atrox.

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of fruitful discussion and analysis of the functional morphology of vertebrates which he has given, have all contributed extensively to enhancing the significance of the present investigation.

To these individuals the author is truly grateful.

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CHAPTER I

INTRODUCTION

It has been forty years since Leverett A. Adams ('15) remarked, "There has been a great neglect of the correlation between osteology and myology. Hundreds of monographs are at hand on both subjects, yet synthetic studies that deal with both and with their interrelationships are extremely rare". And it must be admitted that the same situation exists even today.

There are reasons, of course. First of all, any paper on either myology or osteology which purposes to correlate large bodies of data will of its very nature stir up comment, much of it critical. The well-known attempt to correlate jaw muscles, which the above quotation prefaces, has long been the target of critical commentary by specialists in various phases of the cranial region of vertebrates. But is a practically impossible task to synthesize data from widespread sources and yet avoid slighting or misinterpreting the work of the investigators in these less extensive fields which make up the overall summary.

Secondly, the existing body of data will not of its very nature allow accurate correlation of widely separated forms, as Adams has attempted to do. For, though the material on myology or osteology is extensive, there does not yet exist an accurate correlation of myological data with osteological data in enough individual forms, as Adams himself admits. Yet correlations

such as these are necessary before general correlations of diversified forms can become practicable. Thus it is little wonder that at present no satisfactory synthesis of widely separated forms is to be had. Hence in the present example, there is little hope of gaining widely accepted agreement regarding the jaw muscles of various vertebrate Classes when the relationships of the individual muscles to the skull are known for only a few genera. Again, there is little likelihood that the muscles themselves will be properly interpreted when the nature of the articulations over which they work is in most instances practically unknown. In short, there is great need for correlative studies of jaw muscles, skull, and articulations in numerous basic forms; only after this has been completed will synthesis on a wide scale, such as that attempted by Adams, be profitable and acceptable to all.

Thus a more thorough understanding of individual forms is needed. In the present instance this will require first of all a thorough knowledge of all the muscles involved in the swallowing mechanism of a given form. Secondly, it will require a thorough knowledge of the osteology and arthrology of the skull and jaw region in this same form. And lastly, it will require a thorough knowledge of the cranial interrelationships of the myology and osteology in this same form; i.e., a knowledge of the <u>functional</u> relationships of the jaw structures. Only after these three aims are attained in numerous individual forms will synthesis of the jaw mechanisms as found in many forms be of real value.

In view of this situation the present investigation into the functional anatomy of deglutition in ophidians was begun. The extraordinary feats

of swallowing have characterized snakes in the minds of most people down through the centuries, and doubtless have contributed to the awe with which snakes are almost universally regarded. That an animal is able to engulf prey larger than its own head seems at first sight impossible, and it is little wonder that the uninformed often remark that the snake must "unhinge its jaws" while swallowing. Even the layman almost instinctively realizes that there must be some special functional modification in the jaw region of snakes, though the above interpretation is morphologically unsound.

Hence we are not too surprised to learn that there have been numerous investigations of the jaw mechanism in snakes. However, a survey of the literature shows that for the most part these studies have been directed toward phylogenetic interpretation of large taxonomic groupings. There have been a number of papers on the descriptive anatomy of bones or of muscles, but rarely both together in the same form. Of necessity, then, functional studies of the swallowing process in snakes are practically non-existent. In view of this it would be quite amazing if proper correlation of ophidian cranial structures had been attained on the ordinal or class level. Hence we find that the present investigation, directed as it is toward a functional interpretation of the swallowing mechanism in snakes, lends itself to providing at least a partial solution of the general problem outlined previously.

The purpose of the investigation is twofold. First of all, the author hopes to clarify much of the work already done. The present studies are the first attempt to interpret previous investigations from the functional standpoint. In myology, notably, there exists a large body of descriptive work, mostly carried out for taxonomic purposes. This is especially true as

regards the jaw muscles. The work is in need of the unifying aid of functional studies such as those now under consideration. Thus the present investigation has a basis in work already completed; our main purpose is to complement this earlier work and extend its applicability.

The second purpose of this investigation is to determine accurately the functional basis for swallowing as it is found in snakes. The subject, first of all, is of general zoological interest. Secondly, and more important, it will contribute to the understanding of the evolutionary trends in various types of reptilian jaw mechanisms. Hence these studies will be a contributory factor in interpreting ophidian phylogeny.

Thus, in summary, the author hopes in the present study to form a new basis for the re-evaluation of the body of available data on the cranial region of snakes; i.e., to reinterpret the significance of the results of other workers from the standpoint of function. In itself this will be of academic interest. More important, the present investigator hopes by this means to throw new light on the complex evolutionary changes in the jaw region of snakes, changes evident from extant as well as purely fossil forms. What is more, he hopes in this manner to establish a more solidly founded basis for future studies in comparative reptilian anatomy, especially as the present work complements or challenges data from other sources. In brief, the author hopes to clarify some fundamental aspects of relationship in this cosmopolitan and well-established suborder of reptiles.

CHAPTER II

REVIEW OF THE LITERATURE

Part I: Osteology

During the course of the last century and a half, numerous investigations have been made on the osteology of head of snakes. Because the workers have approached the subject from different angles, it seems advisable in the present review to categorize their work into several subdivisions, and thus gain an overall picture of the present status of ophidian cranial osteology. It may be noted here that many of the early workers described what they considered to be a "typical" snake. Subsequent investigations have shown that in many instances these workers were studying primitive or specialized, rather than recent and generalized, forms. The following categories are based on current views of the relationships of various Families.

1. The Ophidian Skull in General. Though by no means the earliest worker, Boulenger in his monumental Classification of the Snakes in the British Museum (1893-1896) was the first to outline in broad terms the general features of the skull as found throughout the suborder. His relatively detailed descriptions, together with numerous drawings of the entire skull, make this an important source work. Phisalix ('14, '22) has analyzed the cranial anatomy of numerous types of snakes, especially as regards its bearing on the develop-

ment of the venom apparatus; the studies on osteology are of less importance than other features of her work. Williston ('14, '25) makes rather frequent reference to snakes in general in several of his palaeontological papers; he seldom indicates the forms he has in mind. However, it would appear from several indirect references that he is considering the Boidae, which is understandable in view of the relatively extensive fossil record and large size of most of these forms. Radovanovic ('37) has published an extensive paper on the cranial osteology of snakes, emphasizing familial differences. Since almost all of his figures are from the dorsal aspect, his work complements the numerous figures shown in lateral aspect by Boulenger (op. cit.). Mahendra ('38) based a classification of snakes on cranial characteristics, presenting his data in tabular form; many of his conclusions regarding phylogeny have been questioned in recent years, though the data presented is accepted as accurate. Scortecci ('39) employs photographs to illustrate his review of the snakes of Ethiopia; the main portion of his monograph is devoted to a description of Python.

More recently Bellairs & Underwood ('51) have reviewed the material bearing on the origin of snakes from lizards. McDowell & Bogert ('54) also include extensive data on numerous aspects of the skull of snakes, though emphasis is on scurian-ophidian affinities. Hoffstetter ('38) reviews the fossil record, which of its very nature treats mainly of osteological relationships. It may be noted here that fossil snakes are relatively rare, as compared with other types of reptiles. This is in great part due to the fragile nature of the kinetic ophidian skulls and to the lack of limbs which

would otherwise contribute to a more easy interpretation of the cranial material that is available.

2. Development of the Ophidian Skull. As compared with other vertebrate groups, the embryology of snake skulls has not been extensively investigated. Gaupp ('06) outlined the main aspects of development in several forms. Peyer ('12) described in some detail the embryology of Vipera aspis. DeBeer ('37) treats of several groups, especially Boidae, and singles out many special features for analysis. Brock, a student of DeBeer, has investigated several rather aberrant forms ('29, '32), and notes the general relations of ophidian and saurian embryogeny ('41). Pringle ('54) has compared graded embryos of several widely separated South African forms, including the egg-eating colubrid Dasypeltis, and the viper Causus. In general, relatively little material is available as regards comparative ophidian embryology. Perhaps when a method of obtaining graded series of viviparous snakes is found, results along this line will be more extensive. Clark ('37) has devised a method of obtaining such forms, but his technique has not yet been applied to genera other than Natrix, with which he worked.

3. Cranial Osteology of Primitive Snakes. Much of the early work on the cranial osteology of snakes is based on the Boids, probably because of their large size. Owen (1866) described Boa and Python in some detail, as did Goodrich at a much later date ('30). Williston ('14, '25), Phisalix ('14, '22), Versluys ('12, '37), and DeBeer ('37) all treat of Python. Versluys also discusses Cylindrophis rufus, a specialized primitive snake, which he consider-

ed a typical ophidian form. Brock ('29) also treats of the developmental anatomy of Leptotyphlops, a primitive form. Both the Typhlopidae and the Leptotyphlopidae, families of small burrowing reptiles, have been much discussed since they have long been considered to be near the basal ophidian stock. However McDowell & Bogert ('54) have recently questioned the ophidian relationships of the typhlopids, and placed them in a distant branch of the Sauria. The phylogenetic status of these forms will certainly be challenged by other workers in future years.

4. Cranial Osteology of the Colubrids. Most of the members of the Suborder Ophidia are at present classed among the Colubridae; hence it is not surprising that many workers have investigated the skulls of this group. Huxley (1871), Parker (1879), Gaupp ('11), and Bachstrom ('31) have analyzed in detail the skull of the common European grass snake, Tropidonotus natrix. M. Smith ('51) pictures the skull of Coronella laevis in his book on the herpetology of Britain; the figure was prepared for Smith by Bellairs, who includes a somewhat improved drawing of the same form in his 1951 review of the origin of snakes. Cowan & Rick ('51) discuss some of the cranial osteology of several species of Thamnophis, but the crude sketches included in their paper are far inferior to the careful figures of other workers. The present investigator has presented the descriptive anatomy of the skull of the rat snake, Genus Elaphe, in some detail ('53); a few features of the skull have been reinterpreted in the light of later investigation.

Several specialized colubrids have been described in the literature. Kellicott (1898) used Heterodon in his book on general ophidian anatomy; the

plates of the skull, however, were incomplete and several new and improved figures are included in the reprint published in 1939 by the General Biological Supply House, Chicago. Gans ('52) and Pringle ('54) both treat of the egg-eating snake Dasypeltis, the former in much detail.

5. Cranial Osteology of the Venomous Snakes. Studies on the poisonous snakes, especially the vipers, are quite numerous. McKay (1889) was the first to carry out an extensive investigation of the entire osteology and myology of a snake, employing the Death Adder of Australia (Acanthophis antarctica) for this purpose. His analysis of the muscles is much more extensive than are his osteological findings. Fairley ('29) investigated a large series of Australian poisonous snakes; his work is quite detailed in some respects, and includes some interesting studies of tooth pattern. He also published a complete series of photographs of the Australian proteroglyphs, though unfortunately all views are from the lateral aspect only. Phisalix ('14, '22) treats of Bitis and Causus among others in her book on poisonous reptiles. Pringle ('54) mentions some less important features of Causus.

6. Cranial Arthrology of Snakes. Surprisingly little investigation has been devoted to the kinetics of the ophidian skull. Versluys ('12, '37) has given much space to the movements of the skull in both snakes and lizards, but the remainder of the literature on the subject is scanty. A few workers have mentioned the mechanism involved in erecting the fangs, but the explanations are rather general. Boulenger ('17) and Fairley ('29) discuss the problem in some detail, the former pointing out a number of interesting cor-

relations between the colubrid Xenodon and the solenoglyphs. Gans ('52) discusses at length the functional morphology of the skull of Dasypeltis scabra and the osteological adaptations necessary in this specialized egg-eating genus. Pringle ('54) notes a few points of the cranial kinesis, especially the naso-frontal articulation. In recent years more emphasis has been placed on the significance of the intramandibular joint in snakes, first mentioned by Williston ('14) with reference to the Ophidia. Dunn ('51) notes this articulation as a distinguishing feature between the closely related forms Sibon and Dipsas; in the latter a functional articulation is present, although Dunn does not hazard an opinion on its significance. McDowell & Bogert ('54) re-analyzed the significance of the intramandibular articulation in snakes and its bearing on the origin of snakes from saurian stock.

In general, however, the cranial arthrology of snakes has received scanty treatment in the literature. One of the primary purposes of the present investigation is to analyze this subject and its bearing on osteological and myological modifications in the deglutitional mechanism of snakes.

Part II: Myology

A study of the cranial musculature in snakes is of its very nature a complicated undertaking. Not only is the morphological condition of the muscle groups highly modified from the generalized vertebrate pattern, but the terminology employed by workers in the field has through the course of years become complex in the extreme. There is relatively little agreement among investigators as to the proper name to be employed for a given muscle. This

is not only because of disagreement as regards homology, but because there is no generally accepted criterion for the use of the terms themselves. (Cf. Davis, '36). That unanimity as regards terminology may ever be attained is perhaps too much to hope for. Meanwhile workers in the field will continue to avail themselves of tables of synonymy in their attempt to understand the literature.

Towards this end the present writer has compiled a new synonymy (Appendix B), in which is included the terminology employed by investigators of ophidian cranial myology. As might be expected, there will probably be some disagreement in the future as to the present writer's interpretation of the literature. This will be due chiefly to the fact that different investigators often treat of different Families, and a given term can seldom be satisfactorily applied to all these forms. Nevertheless, it seems advisable to include such information here as an aid, at least, to later understanding of this complex problem.

In the account that follows, the historical data has been subdivided into six main categories. The divisions are made from a regional standpoint, chiefly because previous investigators have for the most part studied muscles on just such a basis. Though other methods of grouping are certainly preferable for critical analysis, this more historical approach seems best for present purposes.

1. Cutaneous Musculature. The first recognized anatomical study of snakes was made by Tyson in 1688. He analyzed the then novel form Crotalus, the rattlesnake from North America. His work on the cutaneous muscles stood

alone for over two centuries until Ruffa ('04) studied the musculature of locomotion in Tropidonotus natrix. The work of these two investigators on the cutaneous muscles is of secondary interest here, and will be considered only with reference to the costocutaneous musculature of the throat region.

2. Axial Musculature. The complicated body musculature of snakes has received extensive treatment in the literature, chiefly in the attempt to analyse ophidian locomotion. The axial muscles have an indirect bearing on the swallowing process in snakes, and will be treated hereafter only as they affect the deglutitional mechanism in the neck region.

Home (1812) dissected and carefully illustrated some of the main axial muscles in Boa constrictor. Mehner's dissertation (1815) is often mentioned by later workers, but the present writer was unable to locate a copy of this admittedly rare work (cf. Meenuer, '35). The famous comparative anatomists Meckel (1826) and Cuvier (1836) both discuss some of the body musculature. Jones (1854) treats of some of these same muscles, evidently obtaining his material directly from Home. Owen (1866) likewise repeats material already known, and contributes nothing that could be called new. McKay (1889) reviews the complete myology of Acanthophis antarctica, but in the absence of detailed figures his textual material is in some respects difficult to analyse. Kellicott (1898) mentions some of the more obvious axial muscles in Heterodon, but adds nothing to our knowledge and leaves many details to be desired. Nishi ('16) and Meenuer ('32, '35) contribute extensive data on the axial musculature in snakes. The latter especially presents a thorough account of the body musculature in many families, including Elaphe obsoleta. Though Meenuer treats

of the muscles in the mid-body region, the present investigator has confirmed the presence of all the muscles mentioned and traced them to their cranial attachments.

3. The Dorsal Trigeminal Complex. This extensive group of cranial muscles has received thorough treatment in the literature, though there is much disagreement on many points. Dugès (1827) was the first to study the head muscles of snakes in detail, and he outlined some of the basic principles of the swallowing process. Several years later Duvernoy (1832) used differences in jaw musculature as a basis of distinction between poisonous and non-poisonous forms. D'Alton (1834) dissected and carefully described the head muscles of Python bivittatus, but the terminology employed by him is unwieldy and usually vague, and it is from his work that much of the later confusion in terms has arisen.

Jones (1854) presents a concise, and seemingly accurate, description of ophidian jaw muscles; however like Owen who followed him (1866) he seems to have obtained his material directly from Duvernoy. Teutleben (1874) is often noted in the literature, but his praiseworthy attempt to homologize vertebrate jaw muscles fails utterly when he comes to snakes, and he seems to have had no first-hand knowledge of the Ophidia. Hoffmann (1885) reviews D'Alton's work, and helped to clarify the latter's confusing terminology. McKay (1889) dissected the musculature of several Australian forms, including the Death Adder, and presents a detailed description of his results. In general he follows the leads of Duvernoy and Owen, with some reference to Hoffmann. McKay's work is the most complete of all the early workers. In 1898 Kellicott contributed a

description of the muscles in the specialized colubrid Heterodon, but his often inappropriate use of terms suggests that he had no knowledge of the literature that preceded him.

At the turn of the century Rosen ('04) described some of the more obvious muscles of the head region, but his drawings are inferior to those of other workers, and his work in general is rather superficial. Hager ('06) was the first to attack the problem with the use of photographs of muscle dissections, but they are poorly labeled and rather minute in their published form. Phisalix ('14, '22) and Adams ('25) both repeated dissections of the head region, stressing especially the trigeminal complex. Adams, however, was more interested in comparing Natrix with Varanus and has omitted material that should not be overlooked in a comparative study. Lakjer ('26) contributed a monograph on the dorsal trigeminal muscles in Sauropsida, and at present it is still considered one of the major works in the field. His treatment of snakes especially is extensive. Fairley ('29) outlined the condition of the muscles in the Australian proteroglyphs, but added nothing particularly new to the subject, and seems to have followed Phisalix closely. Since 1930 Haas (all citations) has presented a series of papers on the dorsal trigeminal muscles in numerous families of snakes, but since he bases his phylogenetic interpretations entirely on this one muscle group not all students of taxonomy are willing to accept his conclusions. Radovanovic ('35) has contributed an extensive study of the head muscles in numerous forms, including many of the common colubrid genera (Thamnophis, Natrix, Zamenis, etc.). The emphasis is on the infra-familial level and he unfortunately discusses only some of the more superficial muscles.

Scortecci ('39) presents data on the head muscles of Python; he also includes many fine photographs of the head region of several Ethiopian forms. In 1944 Kesteven published another section of his voluminous study of the cranial muscles of vertebrates in which he treats of some muscles of Python variegatus and the elapid Pseudechis porphyriacus. But he persists in using his own terminology with vague references to Fairley and Hoffmann, and in general his work is difficult to interpret in the absence of bibliographical data.

More recently the cranial musculature of three species of Thamnophis has been compared by Cowan & Mick ('51), but it would seem that their data has more generic than specific value. The speculative portion of the paper is stimulating, however, and will be discussed more fully in later chapters.

The present investigator has described in detail the trigeminal complex as it occurs in Elaphe, and further studies have indicated that no modifications in the original description of the dorsal trigeminal field is required.

4. The Intermandibular Musculature. Relatively little work has been done with the muscles of the anterior throat region. D'Alton (1834), Duvernoy (1832), Jones (1854), Hoffmann (1885), Kellicott (1898), and Hager ('06) all mention some of the intermandibular muscles in their work on cranial myology. However in all instances the data shows wide variation, probably because of the fact that the muscles of the region are minute and interrelated in a complex manner.

Göppert ('06) has discussed several of the tracheal muscles as they occur in Tropidonotus natrix. Adams ('25) mentions some of the muscles of the region, as does Fairley ('29). The volume by Edgeworth ('35) on the cranial muscles of vertebrates treats of the throat muscles from the standpoint of embryology. Gnanamuthu ('37) has presented an extensive paper on the tongue musculature of reptiles, but his data on snakes is difficult to interpret in the light of other studies, probably because he confines himself to the primitive Python molurus and the aberrant Helicops schistosus. Scortecci ('39) treats of some of the throat muscles in Python. Kesteven mentions both Python and Pseudechis in his 1944 paper, but as in the case of the trigeminal complex his analysis of the intermandibular musculature is unique. Cowan & Hick ('51) and the present investigator ('53) have described the throat muscles in Thamnophis and Elaphe.

5. The Posterior Throat Region. This portion of the cranial musculature has been scarcely investigated at all. Ruffa ('05) described the costocutaneous musculature, but did not define its cranial limits and variations. Meesner ('35) confined himself to the axial muscles of the mid-body region. Lubosch ('38) has made a few comments on the serial homology of several muscles of the neck region, but presents little descriptive material that aids in interpreting his views. Edgeworth ('35) notes a few relationships in the posterior throat region, but his discussion lacks the thoroughness we would desire for our purposes. Cowan & Hick ('51) describe several muscles in this region as they occur in the garter snakes; however it appears that they were not as careful with their dissections here as in the intermandibular area. The pres-

ent investigator ('53) has mentioned some of the more obvious muscles of the neck region in Elaphe.

6. The Motor Nerve Distribution to the Cranial Muscles. The peripheral distribution of the cranial motor nerves in snakes has received only passing reference in the literature. Owen (1866) shows some of the general distribution in Python, but the illustration shown is of a general dissection and it is practically impossible to trace the pathways in any detail. Phisalix ('14, '22) presents some of Owen's data, but unfortunately applies the conditions found in Python to all snakes. Adams ('25) makes a few passing references to the fields of innervation in Natrix. The following year Lakjer ('26) noted some variations in the distribution of the motor divisions of the trigeminal, but did not trace the nerves to their muscular terminations. Papez ('29) presents a little data on the motor nerves in snakes, mostly concerning the intracranial relationships. Edgeworth ('35) and Gnanamuthu ('37) both refer in passing to some aspects of the innervation of the throat and tongue musculature, but the references are very general. Kesteven ('44) notes the general innervation of some of the muscles, but gives no indication of the pathways. More recently Pringle ('54) has noted a few features of the nerves in the otic region of some South African snakes, laying stress on the intraosteological relationships.

In general we may summarise the work on ophidian cranial myology as follows. There has been a large amount of descriptive anatomy of many genera of snakes. However only the Australian Death Adder has been described with

any degree of completeness prior to recent work on the garter and rat snakes, Thamnophis and Elaphe. Anatomical studies on some portions of the cranial musculature (viz. the dorsal trigeminal complex) are extensive, and comparative work is already far progressed. Other portions of the cranial area (viz. the hyoid and posterior throat region) are scarcely mentioned at all in the literature, much less described in detail.

With the exception of McKay's (1889) work on the Death Adder and the present investigator's ('53) studies on Elaphe, there is no relatively complete descriptive work on both the cranial osteology and myology of a single genus of snakes. Hence it is understandable that no thorough analysis of the functional morphology of swallowing in snakes has yet been published. Hitherto the investigations on ophidian cranial myology have been directed toward solving problems of homology and phylogenetic relationships. But though the references to cranial muscles in snakes are numerous, data on the functional aspects of these muscles are subordinated to descriptive relationships.

In order to further appreciate the significance of comparative cranial myology in snakes, it is essential to have a clear concept of the functional aspects of deglutition. The present investigation is directed toward this end.

CHAPTER III

MATERIALS AND METHODS

Sixty-eight specimens have been used in the present investigation exclusive of the osteological material. These include sixty-five specimens of the Family Colubridae, in addition to the head region of three juvenile specimens of Crotalus horrus, Family Crotalidae. The material is listed in Appendix C. All specimens were keyed out before dissection in Schmidt & Davis ('41). The twelve accessioned specimens of Elaphe from the Chicago Natural History Museum and the four specimens from the Lincoln Park Zoo, Chicago, were described by the author previously ('53), but have been re-checked during the course of the present investigation. The accessioned specimens were dissected on the right side only in order to preserve the left side for taxonomic purposes.

Twenty-one specimens of Elaphe obsoleta quadrivittata and the four specimens of Heterodon contortrix contortrix were purchased live for the functional studies. These specimens were kept at room temperature in glass-front wooden boxes 18 X 10 X 10 inches in size. The larger specimens were housed singly, but at times the smaller specimens were kept two to a box. It was found that solitary housing not only reduced mite infestation, but also prevented competition for food as often happens when two or more specimens are kept in relatively close quarters. The live specimens of Elaphe were maintained on white mice, live or fresh-killed, and were fed on the average of

two mice per snake every twelfth day. The four specimens of Heterodon refused to eat in captivity, though frogs and mice (both live and fresh-killed) were provided; their ordinary diet of toads could not be provided at the time. All of the specimens were supplied with ample water at all times; the container was large enough to allow the specimens to coil up inside, which they often did especially after eating.

For reasons indicated in the previous chapters, a genus of the Family Colubridae was chosen for the functional aspects of the present study, thus avoiding the primitive characteristics occurring in forms such as Python and Boa, and the specialized features which are to be found in the Elapidae and Crotalidae. The colubrids make up most of the vast assemblage of the world's harmless snakes, and include some 276 genera (Schmidt, '50). The genus Elaphe comprises about four dozen species of cosmopolitan distribution. Because of this factor the genus was selected as representative of the Family; the morphology of Elaphe is thus most likely to show the typical colubrid condition. The species obsoleta was found in previous studies ('53) to be typical of the genus as found in the United States. Though most of the North American species of Elaphe make hearty captives, Elaphe obsoleta quadrivittata was selected for the present study because of its large size, ready availability, and docile nature; Elaphe obsoleta obsoleta would probably have served as well, but it is not as readily available during the winter months.

The present study has been limited to those aspects of the osteology, myology, and neuroanatomy which appear to be concerned with the deglutitional processes of this generalized ophidian type. The entire skull and

its ligaments, the hyoid apparatus, and some general features of the vertebrae and ribs are discussed. All of the muscles of the cranial region are analyzed with the exception of the ocular muscles and the intrinsic muscles of the tongue and larynx. The axial musculature is treated of only insofar as it has direct bearing on the swallowing process. The musculature of the esophagus is considered outside of the scope of the present investigation; for further data the reader is referred to the work of Rosatini ('35). All of the muscles studied are listed in Appendix A according to the nomenclature used in the following chapters. Data on the motor nerve distribution to these muscles is included in the following pages insofar as it has bearing on the phylogenetic interpretation of the muscle groups.

Six major modes of investigation were employed in the course of these studies. In most instances several of these methods were used for each specimen.

1. Direct Observation. Throughout the course of the investigation numerous observations were made by the writer on the actual swallowing process. Live mice were ordinarily used, but fresh-killed mice, mouse skins stuffed with ground meat, and even ordinary frankfurters were employed at various times. Notes were taken during and immediately after the observations, and later correlated with data obtained by other means. In one live specimen the mandibular branch of the trigeminal nerve was sectioned at the dentary foramen in order to determine whether denervation of the intermandibular musculature might have any significant effect on the jaw action. However the specimen refused to eat, and after six months no data is available.

2. Dissection. Skeletal preparations, both articulated and disarticulated, have been made. The skulls were roughed out by hand and then boiled in a trisodium-phosphate solution to which soap had been added. Articulated preparations were removed from the solution after the operation had proceeded to the stage in which the soft parts were somewhat macerated, and then finished by hand under the dissecting microscope. All live material was prepared for dissection immediately after death by injecting seventy per cent alcohol into the subcutaneous spaces, the various large muscle groups, and in the major fascial planes; there was no appreciable shrinkage of tissue. A hypodermic syringe and a #27 needle was used for this purpose, care being taken to avoid excess pressure which would distort the specimen. The binocular microscope was used extensively in dissection. In a few instances where gross dissection was not a sufficiently delicate method to show relationships, microscopic slides were prepared. The material was fixed in alcohol, paraffin embedded, serially sectioned at ten micra, and stained with hematoxylin and eosin.

3. Electrical Stimulation Studies. This method of investigation was used to test the action of individual muscles and synergistic muscle groups, and to determine the innervation pathways. A one per cent solution of Nembutal in physiological saline was used as an anesthetic, and injected intraperitoneally. The technique employed by Franklin ('45) for Natrix taxispilota was found satisfactory for Elaphe, and accordingly administered: 1cc/kilogram body weight. During the operations care was taken to keep the field sufficiently moist with physiological saline (Turtle Ringers). During dis-

section of the otic region it was found necessary to ligate the carotid artery a short distance behind the head; it proved impossible to carry out dissection in this area without rupturing some of the thin-walled blood vessels which are here especially numerous.

Stimulating electrodes were prepared from steel insect pins, and a finely-controlled electrode mount was fashioned from the rack-and-pinion mechanism of an ordinary compound microscope. This semi-micro arrangement was found necessary because of the limited area of operation and the extreme minuteness of some of the motor nerves. Current was supplied from an ordinary laboratory inductorium and battery arrangement. These experiments were all carried out under the binocular microscope. With proper care, muscular response could be elicited for as long as nine hours following ligation of the carotid artery.

4. Analysis of the Tooth Pattern. Since the spatial relationships of various parts of the dentiferous bones are of importance in the study of deglutition, a method was devised to analyze the tooth pattern. For this purpose ordinary frankfurters were used as food. A small piece of skin from a fresh-killed mouse was securely tied to one end of the food; this served as an olfactory stimulus and caused the snake to begin immediately at the end of the frankfurter instead of first grasping it in the middle. After the snake had swallowed several frankfurters in succession, it was sacrificed and the ingested material recovered. It was found that forced regurgitation caused additional tooth marks on the frankfurter.

The recovered food was immediately washed in running water to remove foreign materials, and then placed in a ten per cent aqueous solution of aniline blue for twenty-four hours. Following a second washing to remove excess stain, the material was dried and studied under the binocular microscope. Since the stain has only a slight effect on the casing of the frankfurter, the tooth pattern stands out rather clearly. During the staining period the dye penetrates the small holes made by the teeth in the casing, and stains a small area of the meat itself. Tissue paper tracings of the spots permits transfer of the pattern from a curved to a flat surface. The pattern was then transferred a second time to machine duplicator stencils ("hectograph") and a sufficient number of copies run off to allow for various forms of analysis. A sample of the final copy is included here as Appendix D.

Experiments were also made using commercial liquid plastic (transparent Krylon). Five coats were sprayed on the frankfurter, allowing each to dry thoroughly. Since the plastic does not stain, the colored spots are indications of the tooth pattern and not the irregularly-spaced minute holes that invariably occur in the casing. However it was found impossible to keep the plastic coating tightly applied throughout the length of the frankfurter during the swallowing activities; hence a continuous pattern is not obtained by this method. Attempts to remove the plastic in a single sheet for analysis were unsuccessful.

The method has been described in detail because the technique has not been hitherto attempted. It should be noted that the results obtained are by no means as diagrammatic as might be thought, and that some care is neces-

sary in order to find the pattern made by the minute teeth of the snake. Care is also required in analysing on a plane surface the data obtained from a curved surface. However the method does show some of the interrelationships of the dentiferous bones, and when the results are compared with data obtained from other sources of study there results a more complete picture of functional relationships.

5. Cinematographic Techniques. A mirror arrangement was prepared in order to obtain simultaneous movie recordings of the dorsal, lateral, and ventral aspects of the snake during the swallowing process. However, although the mechanical features were proven adequate for the purpose intended, the specimens were greatly disturbed by the reflections in the mirrors and especially by the transparent glass plate on which they lay apparently suspended in mid air. Numerous attempts were made over a period of several months, but without success. Tabs of adhesive tape were placed over the eyes of the snake in hope that this might allay their panic, but this appeared to confuse them even more. Two or three weeks of starvation was not adequate to stimulate them to eat under these conditions, although they promptly took food when returned to more familiar surroundings.

6. Cinefluorographic Techniques. This recently-developed procedure was found useful in interpreting the activities of various bones of the cranial region during swallowing. The films were made during the course of two visits to the University of Rochester, New York, in cooperation with the staff of the Department of Radiology of that institution. Mouse skins stuffed with ground

horsemeat were used as food to avoid the shadows produced by the bones of live or fresh-killed prey. The films were taken at 64 frames/second, and for study were projected at 16 frames/second. Single frame analyses and tracings were also made using a frosted plastic screen. (Cf. Appendix E.)

The results of all the modes of study were analyzed separately and together, thus providing evidence from numerous sources. Taken as a whole, this material has contributed to the formation of a composite picture of the functional aspects of deglutition in the generalized colubrid Elaphe.

CHAPTER IV

MORPHOLOGICAL DESCRIPTIONS

Section One: Osteology and Arthrology of the Head Region

The ophidian skull is characterised by a high degree of kinetism, or freedom of movement of the palate bones with reference to the cranium; this condition is especially prominent among the colubrids. Kinetism is to be distinguished from streptostylism, a term restricted in meaning to freedom of movement between the quadrate and other bones of the cranium; this characteristic is found in many eosuropsidean forms.

Snakes may be distinguished from lizards in general on the basis of the location of the main transverse axis of movement of the cranial roofing bones. The metakinetic skull of most lizards allows movement between the parietal and supraoccipital bones, with relatively little movement at the fronto-nasal region. The mesokinetic skull of snakes, on the other hand, has the main axis of movement at the fronto-nasal articulation, with a firm syndesmosis between the parietal bone and the bones of the posterior cranial region. The absence of an epipterygoid bone in snakes is correlated with this condition.

Kinetism, streptostylism, mesokinetism, and the general looseness of the cranial bones all contribute toward making an analysis of the swallowing mechanism a complex undertaking. In order to facilitate understanding of functional relationships, it is necessary to divide the head region into functional

components. "Functional components", as used here, refers to the primary functional divisions of the skull as a whole; in many similar investigations this type of division is referred to as "functional units". In the present paper this last term is restricted in meaning; "unit" refers to any individual bone of a functional component that is independently movable with reference to the other bones of the component. The recent work of van der Klaauw ('52) has emphasized the use of the term "functional component" as applied to the vertebrate skull.

Seven functional components are here distinguished: axial, cranial, nasal, palato-maxillary, squamo-quadrate, mandibular, and hyoid. The palato-maxillary, squamo-quadrate, and mandibular components are bilateral from the functional as well as from the anatomical standpoint. Each of the seven components is in turn made up of individual units which are movable with reference to the other osseous elements of its component. It must be stressed that the division into components is merely for convenience in description of function, and does not imply that either the component as a whole or the individual bones which make it up always act together in any given function.

Part One: The Osseous Components of the Head Region

1. Axial Component. Detailed discussion of the anterior vertebrae is outside of the scope of the present investigation; the reader is referred to the papers of Mosauer ('32, '35) for an exhaustive treatment of the general anatomy. In Elaphe short ribs are found on vertebrae 3 and 4; the first full-length rib is on the fifth vertebra. The ribs extend postero-laterad to the

edge of the gastrostegae, where they expand slightly into spatulate cartilagenous end-pieces; there is no fusion of the adjacent vertebrae.

2. Cranial Component. The cranium proper is composed of a parietal, supraoccipital, and basioccipital bone, and paired exoccipitals dorsally and posteriorly; the unpaired sphenoid bone lies ventrally; paired prootic bones are the only members of the otic complex visible from the lateral aspect; paired frontal, postfrontal, and prefrontal bones complete the cranial component anteriorly. To these may be added the columella auris which extends postero-laterally from the prootic region on each side. With the exception of the pre- and postfrontal bones, which allow a slight degree of movement, the bones of the cranial component are all sutured firmly to each other to provide a solid housing for the brain. Though the cranium is pierced by numerous foramina, only those concerned with the motor nerve distribution are discussed here.

The ossa occipitalia (figs. 1, 2, 3, 14) consist of the usual four elements: supraoccipital, basioccipital, and paired exoccipital bones. The os supraoccipitale (SuO) lies dorso-anteriorly and does not contribute to the border of the foramen magnum. The os exoccipitale (ExO) on either side forms the superior, lateral, and most of the inferior border of the foramen magnum; it also contributes to the lateral part of the occipital condyle. The os basioccipitale (BaO) forms most of the prominent condyle and extends ventrad beneath the overlying squamosal bone. The occipital bones serve for the attachment of several of the axial muscles, to be described in Section Two. There are several small foramina for twigs of the hypoglossal nerve in each

exoccipital bone; the largest of these is shown in Figure 14.

The os parietale (Par; figs. 1, 2) is a large, shield-shaped bone which forms the roof of the brain case and extends ventro-latered to the lateral edges of the os sphenoidale. The mid-dorsal portion is in direct contact with the overlying scutes. The postero-lateral part is concave, forming a dorso-lateral fossa which serves as parietal attachment of the adductor mandibulae muscle group. The infero-lateral portion is slightly convex; from this area arises the broad M. levator ossis pterygoidei. A small foramen in the postero-inferior surface of the bone allows passage of the motor nerve to this muscle; this foramen is the only one of any size in the entire wide expanse of the parietal bone. The os parietale articulates with the os supraoccipitale dorso-posteriorly, with the ossa prootica latero-posteriorly, with the os sphenoidale inferiorly, with the ossa frontalia anteriorly, and with the ossa postfrontalia antero-laterally. The orbital portion of the parietal bone forms the posterior border of the optic foramen.

The os sphenoidale (Sph; fig. 3) is a long longitudinally-directed bone which forms the entire basal portion of the brain case from the basioccipital bone rostrad. It lies chiefly in the horizontal plane, extending somewhat vertically only in the otic region. The embryological divisions of the sphenoidal complex are indistinguishable in the adult specimens. From the surface of the sphenoid bone arises the major portion of the constrictor dorsalis musculature. A large foramen in the postero-lateral surface of the bone receives the anterior sphenoidal nerve as it re-enters the cranial cavity. This nerve passes rostrad within the cranium and reappears via a smaller for-

amen in the sphenoid bone near the origin of the retractor ossis pterygoidei muscle. The sphenoid bone articulates with the ossa basioccipitale, prooticum, parietale, and frontale on either side, and is in close apposition to the nasal complex anteriorly. It may be noted that none of the axial muscles extends forward sufficiently far to find insertion on the sphenoid bone.

The os prooticum (PrO; fig. 1) on either side is a fairly large, somewhat circular bone which fills in the area between the os parietale anteriorly, os exoccipitale posteriorly, and basioccipital bone inferiorly. It contains several important foramina (figs. 20, 21). The trigeminal nerve employs two of the larger openings as it passes from the brain case; these are termed here the anterior and posterior proctic foramina. Between the foramina is a prominent bridge of bone, especially apparent in a cleaned skull. The two foramina lie at the dorsal end of two broad fossae which extend, respectively, antero-ventrad and postero-ventrad from the foramina on either side of the bridge. The facial nerve leaves the skull via the posterior foramen of the os prooticum, in company with the mandibular division of the trigeminal nerve and portions of the carotid artery distribution; the seventh nerve however is separated off intracranially by a thin plate of bone. The anterior foramen is for the maxillary division of the trigeminal nerve, and does not give passage to any motor nerves to the muscles. Other foramina which dot the surface of the os prooticum are for small blood vessels.

The columella auris (Col; figs. 1, 14) is a thin, narrow rod of cartilage extending postero-latered from a circular footplate covering the foramen ovale between the exoccipital and prootic bones. The inner ear lies

posterior to the os prooticum and deep to the columellar footplate. The prominent jugular foramen, from which pass many of the cranial vessels and nerves, lies posterior to the foramen ovale between the prootic and exoccipital bones and the deeper-lying inner ear. A discussion of the inner ear and the otic complex is outside of the scope of the present investigation.

The os postfrontale (PoF; fig. 1) on either side is a narrow strip of bone which forms the posterior border of the orbit. It articulates with the parietal bone in a loose syndesmosis which allows a slight degree of movement along a parasagittal axis.

The paired ossa frontalia (Fro; figs. 1, 2, 4, 5) are broad and articulate extensively and firmly with the parietal bone. The median downgrowths of the frontal complex are in close apposition at the ventral midline where they articulate with the os sphenoidale and thus separate the orbits from each other. The downgrowths, or descending laminae, form the anterior border of the optic foramen on either side.

The os prefrontale (PrF; figs. 1, 2) forms the antero-lateral limit of each orbital cavity, and articulates directly only with the frontal bone; in this region a slight amount of movement is possible along an axis extending postero-laterad from the anterior edge of the frontal bone. A prominent foramen in the orbital surface of the prefrontal bone gives passage to the lacrimal duct; vd. Figure 31.

3. Nasal Component (Figs. 1, 2, 3, 4, 6). This component consists of the premaxilla, and paired vomers, ossa nasalia, and septomaxillae. All are firmly joined to each other and function as a single unit.

The premaxilla (PrM) is a T-shaped bone at the anterior end of the upper jaw region; it is edentulous in Elaphe, and lacks any direct contact with the os palatinum or the maxilla. It articulates with all the bones of the nasal complex.

The os nasale (Nas) on either side consists of a dorsal transverse lamina and a narrow infero-median septum, which together form the median and dorsal sides of the nasal passage. The nasal bones articulate with the premaxilla anteriorly, the septomaxillae ventrally, and with each other in the septal region.

The septomaxillae (Sep) are wedged between the nasal bones and the vomers. Each consists of a narrow median septum and a much broader horizontal lamina, which curves dorsad laterally thus forming the ventral and lateral sides of the nasal passage, as well as the anterior portion of the roof of the underlying Organ of Jacobson.

The vomers (Vom) make up the ventral surface of the nasal complex. Each vomer consists of a broad median septum and a postero-lateral cupola which houses part of Jacobson's Organ. The vomers are notched posteriorly, the superior process taking part in the frontal articulation and the inferior process serving as the insertion for the retractor vomeris muscle.

The median fused septa of the paired nasal, septomaxillary, and vomerine bones form a continuous structure which divides the nasal component bilaterally posterior to the unpaired premaxilla.

4. Palato-maxillary Component (Figs. 1, 3, 31, 32). Each half of the palato-maxillary complex consists of a pterygoid, ectopterygoid, maxillary,

and palatine bone; only the ectopterygoid bone is edentulous.

The maxilla (Max) is columnar shaped, flattened somewhat in the vertical plane, and bowed medially in the nasal region. Teeth occur throughout its entire length; they are curved caudad and a bit mediad. At the levels of the pre- and postfrontal bones a shelf-like process extends mediad and slightly ventrad. These palatine and ectopterygoid processes of the maxilla are for ligament attachments, one of which is the intramaxillary ligament which extends between the processes parallel to the shaft of the bone. This ligament prevents inward bowing of the maxilla during opening of the mouth (Chapter V).

The os palatinum (Pal) is also columnar in shape with a slight flattening in the vertical plane; the teeth all point directly caudad, the single tooth row extending throughout the length of the body of the bone. A large, antero-medial process extends toward the midline and forms the dorsal arch of the internal choana. In this same area a lateral maxillary process extends toward the palatine process of the maxilla; the two are joined by a stout palato-maxillary ligament. This ligament is rather loose, but of importance in controlling rotation of the maxilla and the os palatinum during the swallowing process. Its extensive length also permits these two bones to act independently over a relatively greater range of movement, thus adapting this area to variations in the size and shape of the prey.

The os pterygoideum (PtG) forms a posterior continuation of the palatine bone. Postero-laterally it expands into a broad vane which curves outward toward the quadrato-mandibular articulation. The vane is twisted around its long axis at about a 20° angle in such a way that this area of the bone

presents a dorso-medial and a ventro-lateral surface (seen in cross-section in Figure 28). The body of the bone, which bears a row of small, caudally-directed teeth articulates with the os palatinum in a saddle joint which has a main transverse axis and a secondary vertical axis. Rotational movement is thus transmitted directly from the pterygoid bone to the os palatinum around a longitudinal axis, although the shafts of the two bones do not remain in a straight line during the swallowing process (Figs. 33, 35).

The os ectopterygoideum (EcP) is short and flattened, and articulated proximally with the dorso-lateral surface of the pterygoid bone at about the mid-point of the latter. The articulation is a freely-movable plane joint which allows the distal end of the ectopterygoid bone to swing rostrad or caudad in the horizontal plane. The looseness of the capsule permits a slight degree of dorso-ventral movement as well, but forces the ectopterygoid bone to follow the pterygoid bone when the latter is rotated about its longitudinal axis. At its distal end the ectopterygoid bone is flattened in the horizontal plane, and curved slightly ventrad around the dorsal surface of the maxilla. The articulation at this point is basically a horizontal plane joint. However the fibers of the capsular ligament are more extensively developed at the ventro-medial corner of the articulation, where they extend from the distal end of the ectopterygoid shaft to the ectopterygoid process of the maxilla (Fig. 30). This ectopterygoid-maxillary ligament helps rotate the maxillary teeth mediad when the ectopterygoid bone is adducted.

5. Squamo-quadrate Component (Fig. 1). The squamosal and quadrate bones make up this simple, but functionally important, complex.

The os squamosale (Squ) is a fairly large, flat, moderately elongated bone. It articulates with the parietal bone anteriorly and overlies the superior extent of the os prooticum to which it is closely applied but not firmly attached. The squamo-quadrate articulation is a plane joint which allows limited movement of the quadrate bone in the parasagittal plane.

The os quadratum (Qud) is flat and somewhat elongated, expanded at either end to articulate with the os squamosale proximally and with the mandible distally. The proximal end is flattened antero-posteriorly at the squamosal articulation, and the distal end medio-laterally at the mandibular articulation; this is brought about by a one-quarter torsion in the shaft of the bone, and modifies the muscle attachments accordingly. The torsion forms an antero-medial and a postero-lateral surface.

The os squamosale has long been the center of lengthy discussion regarding its phylogeny. Broom ('24) and Brock ('32), as well as McDowell & Bogert ('54), call this element from which the quadrate bone is suspended the tabular bone; the lateral position of the quadrate bone at the squamosal-quadrate articulation is the chief argument in favor of this theory. Versluys ('37) and Bellairs & Underwood ('51), on the other hand, refer to it as the supratemporal bone. Whatever its status, the present writer prefers to retain the most commonly used name until more conclusive evidence for a change is presented.

6. Mandibular Component (Figs. 1, 7-12). Four bones can be recognized in the adult mandible: ossa compositum, angulare, spleniale, and dentale. Of these only the last bears teeth.

The compound bone (CmP), or os compositum, makes up most of the proximal half of the mandible, including the condylar region, mandibular fossa, and the prominent medial lamina. The os angulare (Ang) is a sliver of bone firmly sutured to the compound bone near its antero-medial end. The anterior end of the os angulare lies caudal to the anterior end of the os compositum; this last is referred to herein as the lateral process of the compound bone. The os dentale (Den), which makes up most of the rostral half of the mandible, bears two posteriorly-directed processes. The superior-lateral process supports the proximal one-third of the tooth row which continues rostrad to the tip of the mandible. The inferior-lateral process does not extend as far posteriorly, and covers a part of the infero-lateral surface of the compound bone when the mandibular bones are articulated. The os spleniale (Spl) is a minute splinter of bone located on the postero-medial end of the body of the dentary bone, to which it is firmly sutured. The Meckelian fossa opens medially between the dorsal surface of the os spleniale and the lower edge of the dentiferous ridge of the dentary bone.

The splenio-dentary articulates with the compound-angular complex in a complicated manner (Figs. 11, 12). The articulation is basically a poorly-developed ginglymous joint. Ligaments and osseous processes limit the movement of the splenio-dentary bones around a vertical axis; the vertical arrangement of the articular facets prevents movement around the other axes. Intramandibular movement, then, is thus restricted to the vertical axis passing through the point of contact between the splenial and angular bones; a facet of the dentary bone in this region takes part in the articulation dor-

sally. Adduction of the splenio-dentary segment is limited by the capsular ligament which loosely binds the lateral process of the compound bone to the two lateral processes of the dentary bone anterior to the vertical axis. Adduction of the tip of the dentary bone is also limited by the broad dentary-compound ligament which forms a syndesmosis between the superior-lateral surface of the compound bone and the ventral edge of the superior-lateral process of the os dentale. Independent abduction of the tip of the dentary bone is prevented by the lateral overlapping of the lateral process of the os compositum, which extends to a point anterior to the splenio-angular axis of rotation. From the resting position, then, the splenio-dentary complex can move toward the midline and back; all its other movements involve the mandible as a whole.

The teeth extend from the anterior to the posterior ends of the os dentale along its dorsal border. Anteriorly the tips of the teeth lie in the same vertical plane as the body of the dentary bone, but along the superior-lateral process the points are directed somewhat mediad as well as caudad.

7. Hyoid Component. The hyoid bone in Elaphe consists of a cartilagenous shield-shaped basihyal and paired ceratohyals which extend caudad for a distance of about twice the length of the skull. The entire apparatus is shaped much like a flattened tuning fork, and lacks all osseous or ligamentous attachments to other parts of the skeleton. The cornua run parallel to the trachea and tongue. The basihyal is bound firmly to the first few gastrosteges but the cornua are free for muscle attachments. The first and second cerato-

branchials, described in Thamnophis by Cowan & Hick ('51) could not be identified in Elaphe, although a muscular inscription in the same area is quite prominent, as shown in Figure 26.

Part Two: Articular Interrelations of the Cranial Components

The seven cranial components described above are closely interrelated both morphologically and functionally. Part Two is divided into ten sections, each treating of the articular interrelations of two of these components.

1. Axial - Cranial Relationships. The atlas bone articulates directly with the os basioccipitale and ossa exoccipitalia in a close-fitting synovial joint. The occipital condyle is formed by the basioccipital bone medially and a small portion of the exoccipital bone on either side. Both vertical and horizontal movements occur at the articulation, but the ellipsoidal condylar formation prevents longitudinal rotation; the latter occurs within the vertebral column itself. There are no extra-capsular ligaments, since the cranial-axial musculature serves to retain the parts in proper relation.

2. Cranial - Nasal Relationships (Figs. 4, 5, 6). The paired frontal bones articulate with the nasal complex in a single joint with two areas of contact, one on either side of the midline. On either side the facets are in a vertical line, all the bones of the nasal complex except the premaxilla taking part in the contacts with the frontal bone. From the ante-

ior aspect (fig. 5) the articular facets of the frontal bone slope postero-mediad; from the lateral aspect (fig. 4) the articular region of the frontal complex is convex anteriorly. The facets of the nasal component are shaped to correspond to the frontal complex at the articulation. This arrangement prevents movement around a vertical axis at the articulation. The transverse axis of the articulation lies posteriorly in the mid-region of the frontal bones; the articular surfaces thus curve around the circumference of a circle whose center is the transverse axis. With this arrangement the nasal component is able to be rotated dorsally and ventrally in relation to the paired frontal bones, but cannot be abducted. The entire articulation is rather loosely held together by the capsular ligament, and some longitudinal rotation around a mid-longitudinal axis is possible.

Movement is further limited by three extra-capsular ligaments. The broad, unpaired fronto-nasal ligament (LFN) extends from the entire dorsal anterior edge of the paired frontal bones to the dorsal-posterior edge of the horizontal laminae of the paired nasal bones; the ligament effectively prevents both lateral and ventral displacement of the nasal component on the frontal bone (fig. 23). Paired prefronto-vomerine ligaments (fig. 32, not labeled) extend from the ventro-medial portion of the prefrontal bone to the most lateral portion of the vomerine cupola. These ligaments are directed parasagittally and, owing to the paired condition of the fronto-nasal articular facets, assist in preventing abduction of the nasal component around the fronto-nasal articulation; in addition they limit dorsiflexion of this component on the frontal bones. Essentially, then, movement of the nasal com-

ponent on the cranial component is restricted to the vertical plane and to slight longitudinal rotation.

3. Cranial - Palato-maxillary Relationships (Figs. 30, 31, 32). The pterygoid and ectopterygoid bones do not articulate directly with the cranial component (kinetism). The os palatinum is situated close to the vomer, but is likewise near the prefrontal bone of the cranial component. It is attached to the os prefrontale by the prefronto-palatine ligament, which extends from the ventro-medial edge of the prefrontal bone to the dorsal surface of the body of the palatine bone adjacent to the maxillary process. The prefronto-maxillary ligament (LPFM) extends from the ventro-lateral edge of the prefrontal bone to the dorso-lateral edge of the body of the maxilla. The postfronto-maxillary ligament (LPSM) is in a corresponding position at the ventro-posterior border of the orbit. Both of these ligaments are long enough to give the maxilla great freedom of movement with reference to the cranium, and are of importance in rotation of the maxillary teeth (Cf. Chapter V).

4. Nasal - Palato-maxillary Relationships (Fig. 32). The maxilla is joined to the septomaxilla by the maxillo-septomaxillary ligament (LMS) which extends from the palatine process of the maxilla to the transverse lamina of the septomaxilla; the ligament parallels the prefronto-vomerine ligament, which joins the vomer to the prefrontal bone. The maxillo-premaxillary ligament (LMP) is an anterior extension of the intermaxillary ligament (LIM), the most lateral fibers of which pass ventro-lateral to the ventro-medially directed palatine process of the maxilla, and continues rostrad to insert on

the postero-lateral edge of the premaxilla. All of these ligaments serve to retain the maxilla and nasal component in proper relation during the swallowing process (Cf. Chapter V).

The os palatinum is joined to the nasal component by a flat ligament which passes from the dorsal surface of the anterior end of the palatine bone to the overlying part of the vomer. This palato-vomerine ligament (LPV), though long in the sagittal plane, is not very wide and effectively binds the anterior end of the palatine bone to the nasal complex, while at the same time providing some freedom of palatine movement around vertical and longitudinal axes. The palatine bone is the main connecting strut between the nasal component and the rest of the palato-maxillary complex; functionally it could be classed as belonging to both nasal and palato-maxillary complexes alike.

5. Squamo-quadrate - Cranial Relationships. The os squamosale is joined to the lateral surface of the parietal bone by a loose plane joint, which limits action of the squamosal bone chiefly to the parasagittal plane, although some movement around a longitudinal axis is possible. The transverse axis of rotation lies about one-third of the distance caudal to the anterior end of the squamosal bone, and thus permits the distal end to rotate through a wide arc. The columella auris extends postero-latered and somewhat ventred to articulate with the quadrate shaft on its postero-medial edge. The columella is too flexible and bound in with muscles, nerves, and blood vessels to have any significant function in the swallowing mechanism.

6. Squamo-quadrate - Mandibular Relationships. The quadrate and mandible are joined in a synovial saddle-articulation which permits mandibular

movement around longitudinal and transverse axes. The synovial capsule is quite extensive; however no check-ligaments are found, since the muscles of the area serve in this capacity.

7. Squamo-quadrate - Palato-maxillary Relationships (Fig. 16). A stout ligament joins the capsule overlying the lateral edge of the quadrato-mandibular articulation with the postero-lateral tip of the maxilla. This quadrato-maxillary ligament (LQM) is subcutaneously situated and sends a slip to the second last superior labial scute.

8. Palato-maxillary - Mandibular Relationships (Fig. 32). The mandible is joined to the palato-maxillary component by a flattened and rather thin connective tissue condensation. This pterygo-mandibular ligament (LPtM) passes in the horizontal plane from the tip and antero-lateral edge of the vane of the pterygoid bone, and is in close apposition to the posterior edge of the vane of the pterygoid bone where the M. adductor mandibulae internus, pars posterior, inserts. The ligament itself inserts on the medial surface of the mandible ventral to the quadrato-mandibular articulation (fig. 17). It is poorly developed, but sufficiently strong to be effective in movements of the mandible in relation to the os pterygoideum.

9. Intermandibular Relationships (Figs. 24, 25). There is no direct connection between the anterior tips of the mandibles. Each dentary bone lies relatively free anteriorly, there being a prominent space dorsal to the mental scutes. The anterior edges of the paired anterior intermandibular muscles bound the area postero-laterally.

10. Hyoid Relationships. As has been mentioned, the hyoid bone in Elaphe is entirely free from osseous and ligamentous connections with the rest of the skeleton; muscle attachments, of course, are extensive.

It is thus apparent that the ophidian skull is modified in such a way that a high degree of kinetism is possible. Control of these movements not only depends on the cranial musculature, but on the extensive ligamentous connections as well. In perhaps no other type of skull are the inter-connecting ligaments so numerous and so essential in coordinating the movement of the bones during deglutition.

Section Two: Myology of the Head Region

As has been pointed out in the previous section, both kinetism and streptostylism are well developed in Elaphe. It might be reasonably expected, then, that the cranial muscles would show a high degree of modification from the basic vertebrate pattern; such is indeed the case. The appearance of neomorphic muscles and muscle slips is directly dependent on the constantly changing osseous interrelationships which occur during the swallowing process, and is necessary if finely coordinated functioning is to be had.

The interrelationships of vertebrate muscles are usually studied from four main aspects: embryological development, innervation, attachment, and function. Embryology provides at least a partial understanding of the basic myological elements which give rise to definitive form. In snakes rela-

tively little has been done along this line, except by Edgeworth ('35).

The nerve supply generally provides an accurate method of tracing homologies, but even here there are drawbacks. It is not yet possible to trace each motor fiber from its origin to the muscle; furthermore, there is no way of being certain that the fibers which make up a given nerve trunk in one form are the same fibers which comprise this nerve in another form. The complicated arrangement of nerves in the ophidian cranio-cervical plexus makes a strictly neurological interpretation of the relations of the throat muscles especially hazardous. In the present investigation the phylogenetic interpretations are not based on motor nerve innervation alone.

A knowledge of muscle origins and insertions is of importance in determining the precise functioning of the attached bones. However for phylogenetic studies it must be borne in mind that these muscle attachments vary extensively, not only in closely related forms, but even on opposite sides of the same specimen. Hence the necessity of examining a sufficiently large number of individuals.

The fourth mode of muscle study is the analysis of function. This method is of importance because morphological patterns directly reflect the muscle action itself. However, as has been pointed out, studies of function are relatively few, mainly because of the numerous variables that enter the picture. The present investigation has as one of its main purposes the clarification of this point in snakes.

In the present chapter the author attempts to correlate his own studies on the innervation, attachments, and functioning of each muscle with

what embryological data other sources provide. It is reserved for the following chapter to correlate the functioning of all the cranial bones and muscles as they actually occur in the deglutitional process.

An intelligible discussion of the muscles of deglutition in Elaphe requires a breakdown of these muscles into smaller groups. The divisions made here are based on studies of the innervation determined by the present writer and the embryological investigations of Edgeworth ('35) on Tropidonotus natrix, a common European colubrid. Owing to the extensive development of kinetism and streptostylism, a division of the jaw muscles on a functional basis is impracticable and will not be employed in the present chapter.

For descriptive purposes the muscles of deglutition may be divided into three chief classes: mandibular, hyoid, and hypobranchial-spinal. These are innervated by the trigeminal, facial, and hypobranchial-spinal nerves respectively. Each class may be subdivided into several groups, each of which consists of one or more parts. The muscles are grouped in tabular form in Appendix A. Limited data on a fourth class of lesser importance (Craniovertebral Musculature) are included chiefly as an aid to orientation in the post-cranial region.

Part One: Trigeminal Musculature

The derivatives of the lateral plate of the head at the level of the second cranial somite (first post-oral somite) compose a large portion of the jaw musculature. In Elaphe the trigeminal nerve, which supplies these muscles, shows the typical colubrid distribution; owing to osseous modifications in the

otic region these relations are not at first sight apparent. This is due chiefly to the development of a wide bridge of bone which spans the true prootic foramen from dorsal to ventral edge, and doubles the number of apertures; in this manner is formed an anterior and a posterior prootic foramen. Accordingly, the trigeminal nerve roots exit from the cranium at two main loci (Fig. 21).

The trigeminal ganglion, which is of course sensory, lies deep within the true prootic foramen, and sends off four main branches. The ophthalmic division (V_1) passes forward within the cranial cavity; it has no motor fibers to muscles. The maxillary division (V_2) exits from the skull through the anterior prootic foramen and continues its course rostrad into the inferior orbital region; it does not supply motor fibers to any of the jaw muscles. The mandibular division (V_3) exits from the posterior prootic foramen and supplies all of the jaw muscles innervated by the trigeminal nerve, except the M. levator ossis pterygoidei. The latter is supplied by a separate division (V_4 of Lakjer, '26) which, after a short intracranial course, exits from the skull via a small foramen in the posterior edge of the parietal bone. The extra-cranial distribution of the nerves to each muscle will be discussed in the appropriate place.

The trigeminal muscle primordium divides into three main parts, each of which in turn subdivides into various muscles and muscle slips. The Mm. Adductores mandibulae extend between the mandible and the neighboring portions of the skeleton; as the name implies, these muscles are concerned with the closing (i.e., elevation and adduction) of the lower jaw. The Mm. constrictores

dorsales, though absent in akinetic skulls, move the palato-maxillary complex and (in Elaphe) the mandible and nasal component as well. The M. constrictores ventrales lie between the anterior ends of the mandibles and serve to draw the latter toward the midline. All three main divisions show extensive splitting and other modifications in Elaphe and snakes generally.

Group One: Adductores Mandibulae
(Figs. 15-21, 32)

The mandibular adductors have been divided in numerous ways by various workers in the field. The adductor externus is the most superficial; it extends from the cranium and quadrate bone to the dorso-lateral surface of the compound bone of the mandible. The adductor medius lies deep to the former, and extends from the quadrate bone to the mandibular fossa and medial surface of the compound bone; it lies entirely postero-lateral to the mandibular ramus of the trigeminal, a point of phylogenetic significance. The adductor internus joins the ectopterygoid-pterygoid arc to the posterior end of the mandible. The adductor profundus is separated from the other adductors by the maxillary branch of the trigeminal nerve.

A. M. adductor mandibulae externus

Pars anterior (AEx, 1). The anterior portion originates from the posterior edge of the postfrontal bone and the anterior end of the dorso-parietal fossa. The fibers converge as they pass ventro-caudad around the angle of the labial scutes. The muscle becomes extensively aponeurotic over the pars posterior of the same muscle, and inserts along the lateral surface of the compound bone. The muscle fibers are confined to the anterior extent

of the aponeurosis. Superficially the muscle is covered by the skin and the quadrato-maxillary ligament; it overlies the Harderian Gland near its origin, and the median and posterior parts of the external adductor further caudad. It is innervated by a separate part of V_3 which passes anterior to the medial part of the external adductor to enter the pars anterior near the middle of its fibrous portion.

Pars media (AMx, 2). The origin is from the posterior end of the dorso-parietal fossa. The fibers converge somewhat as they pass directly ventrad to insert on the dorsal surface of the mandible between the mandibular fossa and the beginning of the dentition. The muscle is covered by the skin at its origin, and by the anterior and posterior parts of the adductor externus at its insertion. It overlies the squamosal bone and the adductor profundus from which it is separated by the maxillary division of the trigeminal nerve and the otic arterio-venous plexus. Innervation is by a separate branch of V_3 which passes directly to the center of the muscle.

Pars posterior (AMx, 3). The origin is from the lateral edge of the quadrate bone and from a longitudinal strip along the antero-lateral surface of the shaft of this bone. The fibers pass antero-ventrad to insert along the dorso-lateral surface of the mandible from the end of the dentition caudad to the quadrato-mandibular joint. The posterior portion is covered by the skin at its origin and by the aponeurosis of the pars anterior of the external adductor at its insertion. It overlies the adductor medius and the adductorexternus, pars media, at the insertion of the latter. This extensive muscle is innervated by several nerve branches which pass from V_3 to enter the muscle on its median surface.

B. M. adductor mandibulae medius. The median adductor consists of a superficial and deep portion, which are closely applied to each other.

Pars superficialis (AM, 1). The larger of the two portions originates from the entire length of the quadrate bone along a median strip of the antero-median surface. It passes antero-ventrad to insert into the entire mandibular fossa. The muscle is covered superficially by the posterior portion of the external adductor, and overlies the deep portion of the median adductor. It is bounded anteriorly by the mandibular branch of the trigeminal nerve which serves as a general landmark in this area. The superficial part of the median adductor is innervated by a branch of the nerve to the external adductor, pars posterior, near the bifurcation of the latter with the main portion of V_3.

Pars profunda (AM, 2). This smaller portion of the median adductor originates from the length of the quadrate bone along a median longitudinal strip of the antero-median surface of the shaft. It passes antero-ventrad parallel to the superficial part, but inserts on the medial surface of the medial lamina of the mandible. This triangular muscle is bounded superficially by the pars superficialis and overlies the extensive nerve and vascular plexus of the otic region. The columella auris remains posterior to the muscle. It is innervated on its medial surface by short branches which arise in company with the nerves to the superficial portion.

C. M. adductor mandibulae internus. The two portions of this muscle are entirely distinct throughout, but are grouped here for embryological reasons.

Pars anterior (AIn, 1). The origin is on the lateral, posterior, and ventral surface of the postarticular process of the mandible. The muscle passes directly rostrad to insert on the distal end of the ectopterygoi bone near the maxillary articulation. Laterally the muscle consists of a tendon which parallels the overlying quadrato-maxillary ligament at its insertion. The muscle is fleshy at its posterior end, forming a prominent bulge visible in the living snake, and tapers gradually as it passes medial to the mandible; it is mostly tendonous anteriorly, although some fleshy attachment to the ectopterygoid bone was found in all specimens examined. The muscle is covered by the M. constrictor colli at its caudal end, by the mandible near the mandibular articulation, and by the external adductors further rostrad. The posterior portion of the internal adductor, the protractor of the quadrate bone, and the M. levator ossis pterygoidei bound it dorso-medially. The infero-medial surface of the muscle is in direct contact with the oral mucosa; the muscle is innervated by a prominent branch of the trigeminal nerve which leaves V_3 in close proximity to the nerve to the external and median adductors, and turns caudad along the dorsal surface of the internal adductor, pars anterior.

Pars posterior (AIn, 2; fig. 13). This short, flat muscle originates on the ventral surface of the pterygoid bone at its posterior end, and passes laterad to insert on the ventro-medial edge of the compound bone of the mandible. The muscle is fibrous throughout. It is bounded dorsally by the pterygoid bone, and ventrally by the anterior portion of the internal adductor and the oral mucosa. It is innervated by short twigs which pass from

the nerve to the last-named muscle and enter the posterior part on its dorsal surface lateral to the pterygoid bone.

D. M. adductor mandibulae profundus, (APr). This flat, thin muscle originates from the dorso-parietal fossa just anterior to the squamosal-parietal articulation. It passes in a ventral direction to insert into the medial surface of the anterior end of the medial lamina of the mandible. It is covered superficially by the maxillary division of the trigeminal nerve as well as by the median portion of the external adductor. It overlies the parietal bone at its origin, and the M. levator ossis pterygoidei and anterior part of the internal adductor at its insertion. It is innervated by a separate branch of V_3 which leaves the latter near the posterior prootic foramen and enters the muscle near its middle. The muscle itself is ribbon-like and easily lost in dissection; this is quite likely the reason that Adams ('26) failed to note it in Natrix cyclopion, although he specifically looked for it. The present investigator has identified it in Elaphe, Natrix cyclopion, Natrix sipedon, Thamnophis, Coluber, Lampropeltis, and Drymarchon. It has not previously been reported in these genera (except Thamnophis); it seems to be more commonly distributed throughout the colubrids than has been commonly thought.

Group Two: Constrictores Dorsales
(Figs. 13, 15-23)

The dorsal constrictor muscles are concerned mainly with movement of the palato-maxillary component on the undersurface of the cranium. They are not developed in akinetic skulls in which they would have no function (cf. Alligator, Crocodylus, Caiman, etc.). However even in these forms the muscles

have a transient embryonic stage (Anderson, '32). In the Ophidia they reach their highest degree of development, which is of course coupled with the highly kinetic skull of most snakes.

In Elaphe, and the majority of snakes, the dorsal constrictor muscle plate is divided into five parts, which extend in sequence along the dorsal surface of the pterygoid and palatine bones from the postarticular process of the mandible rostrad to the median choanal process of the palatine bone.

A. M. protractor ossis quadrati (PrQud). The quadrate protractor is a flat, thin, triangular muscle. It originates from the midline at the basioccipital region just dorsal to the mucosa, and is joined on its dorsal surface to the ventral aspect of the extensive cranial insertion of the M. transversohypapophyseus. The protractor inserts on the medial surface of the posterticular process of the mandible dorsal to the insertion of the M. adductor internus, pars posterior. Its anterior border overlies the posterior border of the pterygoid bone to a slight degree in most specimens. The cranial vessels, nerves, and the columella auris are all dorsal and posterior to the muscle. Its nerve enters the dorsal surface near its insertion; its proximal course will be described with the nerve to the M. protractor ossis pterygoidei, of which it is a part. The insertion of the muscle is variable among Ophidia.

B. M. protractor ossis pterygoidei (PrPtg). This muscle is also highly variable among the Ophidia. In Elaphe it arises from the midline of the sphenoid bone. Its fibers pass ventro-caudad to insert along the postero-medial surface of the pterygoid vane from the level of the pterygo-ectopterygoid articulation to the end of the pterygoid vane. The muscle is bounded

laterally by the M. levator ossis pterygoidei and the otic plexus of nerves and vessels. It is innervated by a separate branch of V_3 which originates near the trigeminal ganglion and passes out of the posterior prootic foramen and ventrad in the angle formed by the posterior border of the M. levator ossis pterygoidei and the dorsal surface of the internal adductor, pars anterior. The nerve swings caudad along the dorsal surface of the last-named muscle and enters the M. protractor ossis pterygoidei on its lateral surface; other fibers pass on to supply the quadrate protractor, as described above.

C. M. levator ossis pterygoidei (LevPt). The muscle is fan-shaped, and originates from the parietal bone ventral to the dorso-parietal fossa. The fibers spread ventrad and mediad to insert on the dorsal surface of the pterygoid bone from the pterygo-palatine articulation rostrad to a point caudal to the ectopterygoid articulation. As the origin of the muscle covers a much less extensive area of bone than does its insertion, the fibers vary in direction accordingly. The posterior fibers pass ventro-caudad, the medial fibers ventrad, and the anterior fibers ventro-rostrad. The levator is bounded by the adductors of the mandible and the Harderian Gland laterally, and by the protractor and retractor of the pterygoid bone medialllly. It is innervated by a branch of the trigeminal nerve (V_4 of Lakjer, '26) which leaves the trigeminal ganglion near the origin of V_3 and passes rostrad within the cranium. It leaves the skull through a small foramen in the infero-lateral portion of the parietal bone, and enters the muscle directly.

D. M. retractor ossis pterygoidei (RePtg). The retractor of the pterygoid bone originates from the sphenoid bone immediately anterior to the

origin of the protractor ossis pterygoidei. The fibers pass ventro-laterad to insert on the dorsal surface of the posterior half of the palatine bone. The muscle becomes aponeurotic anteriorly, its insertion continuing rostrad along the posterior border of the choanal process of the os palatinum. The muscle is bounded by the retractor vomeris medially, and by the Harderian Gland and orbit laterally; near the origin the levator ossis pterygoidei partially blocks from view the lateral third of the retractor pterygoidei when viewed from the norma lateralis. The nerve to the retractors of the pterygoid and vomerine bones leaves the nerve to the protractor of the pterygoid bone within the posterior prootic foramen. It passes ventro-mediad within the posterior fossa and re-enters the cranium through the posterior sphenoidal foramen on the postero-lateral surface of the sphenoid bone. Thence it passes directly rostrad to reappear via the anterior sphenoidal foramen which is covered by the origin of the pterygoid retractor. In its course the nerve thus avoids the insertion of the protractor ossis pterygoidei on the sphenoid bone.

E. M. retractor vomeris (ReVom). This small muscle originates in close apposition to the origin of the retractor pterygoidei muscle which bounds it laterally. It extends rostrad, and slightly laterad to the midline of the sphenoid bone. Fleshy at its origin, it quickly tapers to a flat tendon which passes mediad somewhat to avoid the ocular structures. It inserts on the tip of the inferior process of the vomer. The muscle is bounded ventrally by the oral mucosa and the innervation is directly from the nerve to the retractor of the pterygoid bone.

Group Three: Constrictores Ventrales
(Figs. 16, 17, 21, 24, 25)

The ventral constrictors form the true intermandibular musculature of the floor of the oral cavity, but are masked by the rostral development of the extrinsic tongue and tracheal musculature of hypobranchial derivation. The constrictors extend laterad from the median ventral raphe to the mandible; innervation is from the branches of the intramandibular ramus of V_3 which exit from the medial surface of the mandible near the intramandibular articulation.

Though the ventral constrictors are primitively relatively simple in arrangement, in snakes they have undergone extensive modification. This condition is in keeping with the absence of a mental symphasis and consequent independent action of the two mandibles, and the development of an intramandibular articulation. In Klapha three distinct pairs of muscles are found on each side, each of which is divided into two slips. All of the muscles originate rostral to the basihyal.

A. M. intermandibularis anterior. The muscle lies ventral to the dentary insertions of the protractors of the tongue and trachea. It inserts on the tip of the dentary bone along the ventro-lateral edge, and extends postero-mediad. It is innervated by several small nerves which exit from a foramen in the splenial bone and enter the muscle slips on their dorsal surface.

Pars cutaneo-mandibularis (IA, 1). The larger portion of the anterior intermandibular muscle originates along the ventral midline raphe from the level of the anterior end of the larynx to a point about two-thirds of the distance from the basihyal. It lies flat next to the skin ventral to

all the muscles of the area, and is thus the most superficial muscle when viewed from the ventral aspect.

Pars glandularis (IA, 2). This lesser part of the anterior intermandibularis muscle is a separate portion of the rostral edge of the last-named muscle which originates on the dorsal surface of the lateral sublingual gland. To attain its insertion the slip swings ventrad towards the horizontal plane of the cutaneous portion of the muscle; on ventral dissection the division of the two muscle slips of the intermandibularis anterior appears merely as a cleft in the fibers.

B. M. transversus branchialis. This thin muscle originates from the midventral line dorsal to the origin of the anterior intermandibular, and anterior to the origin of the posterior part of the posterior intermandibular muscle. The transversus curves dorso-laterad around the ventro-lateral aspect of the tongue and tracheal structures, and has a double insertion into the buccal floor and the lateral sublingual gland. Innervation is by branches of the nerve to the anterior intermandibular muscle.

Pars mucosalis (TVB, 1). The lateral slip of the transversus branchialis inserts directly into the mucosa about half way between the trachea and the ramus of the mandible.

Pars glandularis (TVB, 2). The smaller median slip passes dorso-rostrad to insert on the dorsal surface of the lateral sublingual gland at a point rostral to the insertion of the glandular slip of the intermandibularis anterior. The transversus crosses the latter dorsally.

C. M. intermandibularis posterior. This muscle is divided into two parts which remain entirely distinct. The parts are separated from each other by the extensive neuro-costo-mandibular muscle; both parts originate from the ventral raphe ventral to the insertion of the transversus branchialis.

Pars anterior (IP, 1). The origin is from the ventral midline between the origins of the transversus and anterior intermandibularis. The muscle tapers gradually as it passes caudo-laterad, and inserts on the medial, ventral, and lateral surfaces of the angular and compound bones between the levels of the proximal end of the dentary bone and the distal end of the mandibular fossa. Innervation is from a short nerve which exits from the mandible through a small foramen in the angular bone and inserts on the adjacent ventral surface of the muscle.

Pars posterior (IP, 2). This is a very thin strap-like muscle which originates from the mid-ventral line between the insertions of the other intermandibular muscles and the anterior tip of the basihyal. Like the anterior portion, it passes caudo-laterad and inserts on the lateral surface of the compound bone between the mandibular attachments of the anterior portions of the internal and external adductors of the mandible. Innervation is by a minute nerve which passes to the muscle from the nerve supplying the anterior portion of the posterior intermandibular muscle.

Part Two: Hyoid Musculature
(Figs. 15 - 21)

The seventh cranial nerve supplies the muscles derived from the lateral plate at the level of the third pre-otic (second postoral) somite. It is

separated within the true prootic foramen of the trigeminal by a thin plate of bone (prefacial commissure), but passes to the exterior through the posterior prootic foramen in company with the mandibular ramus of the fifth cranial nerve. It then swings dorso-posteriorly to the columella auris and supplies the three muscles to be described. Throughout most of its extracranial course it is in very close conjunction with the extensive plexus of blood vessels, and can be separated from them only with difficulty.

Lightoller ('39) has analysed the reptilian facialis matrices in some detail, and divided the muscle derivatives into superficial and deep portions. In Elaphe the latter is represented only by the M. constrictor colli. The MM. occipito-quadrato-mandibularis and cervico-mandibularis are derivatives of the dorsal division of the deep portion. The ventral mandibular and ventral interhyoid derivatives of the superficial and deep portions respectively are not found in Elaphe.

A. M. occipito-quadrato-mandibularis (OQM). This is a short, thick muscle, representing the second levator of Lightoller (L2); it is the chief depressor of the mandible. In Elaphe the muscle originates from the entire postero-lateral surface of the quadrate bone, and inserts on the post-articular process of the mandible chiefly along the dorsal surface caudal to the articulation. Near its origin a connective tissue condensation is continued over the postero-dorsal edge of the squamosal bone at its quadrate articulation; in some specimens a few muscle fibers pass together with the connective tissue onto the squamosal bone. Innervation is by the facial nerve as it passes directly through the body of the muscle on its course to the other muscles mentioned below.

B. M. cervico-mandibularis (CvM). This muscle is very variable in shape. It originates from the nuchal crest over the third to eighth vertebrae, and tapers as it passes ventro-anteriorly to insert into the lateral edge of the distal end of the quadrate bone. In none of the specimens examined was there any mandibular insertion, although attachment to the quadrato-mandibular capsule is typical. The quadrate insertion varies with the individual specimen, and may be limited to the capsule or else extended over the entire distal half of the lateral edge of the quadrate bone; conditions between these extremes are common. The muscle is innervated by twigs which leave the main trunk within the occipito-quadrato-mandibular muscle and pass dorso-caudad to enter the cervico-mandibular at the middle of its deep surface. The muscle is bounded by the axial, cervico-quadratus, and occipito-quadrato-mandibular muscles, and by the constrictor colli superficially.

C. M. constrictor colli (CnC). This muscle is very thin and is subcutaneous throughout its entire length. It is chiefly aponeurotic, with the muscle fibers concentrated mostly along its anterior edge. Its origin is along the nuchal crest from about vertebrae 3-10, but the longitudinal extent of origin is extremely variable. It inserts along the lateral edge of the gastrosteges from the anterior end of the basihyal caudad; its anterior border usually crosses the posterior portion of the mandible, but does not overlap the posterior edge of the posterior portion of the intermandibularis posterior muscle which parallels it closely in this region. Innervation is by the terminal twigs of the facial nerve which enter the muscle near the level of the distal end of the quadrate bone. Electrical stimulation of its

motor nerve indicates that it is a stronger constrictor of the neck region than the scattered arrangement of the muscle fibers might indicate. Electrical stimulation studies also indicate that the minute branches of the spinal nerves which pass to the dorsal-lateral region of the neck are sensory fibers to the skin and not part of the muscle motor innervation; this confirms the hypothesis of Kesteven ('44) regarding the innervation of this muscle.

The presence of an ophidian constrictor colli has been confirmed in Tropidonotus, Coluber, Python, Thamnophis, and Pseudechis, but not other genera. In Elaphe it is invariably extremely thin and can be traced only by approaching it from the opposite side of the specimen. Not only is it entirely subcutaneous throughout its length, but it is masked by the other cutaneous muscles of the area (viz. MM. costocutaneous superiores and inferiores) which insert directly into the constrictor and the overlying skin.

Part Three: Hypobranchial-spinal Musculature

In the Ophidia, as in most vertebrates, the number of metactic somites involved in the formation of muscle primordia and of the occipital region of the skull is not known. It is to be expected, then, that much confusion exists regarding the actual nerve distribution to the muscles derived from occipital and anterior spinal sources. So little embryological work has been done on the head region of snakes that even a general pattern of distribution does not exist. Furthermore, variations in the number and location of the nerve foramina of exit from the skull are common, and do not display a consistent pattern even within a species. For example, Chiarugi (1890) found two

or three hypoglossal foramina in Tropidonotus; DeBeer ('37) found four of them. The glossopharyngeal nerve exits through the jugular foramen in Tropidonotus and Hemachatus according to Pringle ('54), but he also reports that in Dasypeltis, Causus, and Vipera it exits via the recessus scali tympani.

The present investigator's work on adult Elaphe indicates that the ninth, tenth, and eleventh cranial nerves exit via the jugular foramen. The twelfth nerve exits via two main foramina; the anterior foramen is in such close conjunction with the jugular foramen intracranially that the nerve fibers are already mixed at the external opening of the jugular foramen. The posterior hypoglossal foramen is located in the exoccipital bone; outside of the skull the posterior division of the hypoglossal nerve, which exits via this foramen, is joined by a very minute nerve from the first spinal. All of these nerves combine into one large trunk in the otic region. Electrical stimulation experiments gave such varying and unsatisfactory results that other forms of study are required before the derivatives of the various branchial arches can be determined with any degree of accuracy.

Edgeworth ('35) in his work on the cranial musculature of vertebrates has analysed the divisions of the metactic muscle primordia in Tropidonotus natrix, a common European colubrid. The hypoglossus separates from the lateral plate early, and somewhat later gives rise to the hyotrachealis muscle from its posterior end. The main mass continues rostrad to insert on the anterior end of Meckel's cartilage, later dividing into genioglossus and geniotrachealis anteriorly, and the hyoid head of the neuro-costo-mandibularis (the geniohyoid of Edgeworth) posteriorly.

In the following pages the hypobranchial-spinal muscles refer to all the above-mentioned muscles as well as some others of the posterior throat and superficial neck region. The two divisions into glosso-tracheal and cervical group are merely for convenience; more precise groupings must await further embryological studies.

Group One: Glosso-tracheal Musculature
(Figs. 24, 25, 27)

Four muscles make up this group, viz. paired protractors and retractors of the tongue and trachea.

A. M. Hyoglossus (HyGl). The paired hyoglossi are immediately adjacent to each other throughout their entire length. They arise from the medial edge of the posterior tips of the ceratohyals and pass directly rostrad in the horizontal plane dorsal to the basihyal. They blend anteriorly with the intrinsic musculature of the tongue. The anterior portion of the hyoglossi is covered over by the genioglossal sheath. Two principle nerves from the cranio-cervical plexus supply the muscle. One of them enters at the posterior extremity and the other passes forward to about the level of the posterior end of the dentary bone.

B. M. Genioglossus (GnGl). This muscle arises chiefly from the medial surface of the mandible near its tip, at which point it lies dorsal to the anterior intermandibularis. The muscle forms a stout column of fibers which passes directly caudad and then spreads around the lateral and ventral portions of the tongue sheath, to which it contributes a major part. Other fibers pass from the region of the lateral sublingual gland near the midline

to contribute a small part to the muscle sheath. The sheath inserts directly into the hyoglossal at about the level of the quadrato-mandibular articulation. The genioglossus is innervated by a branch of the anterior division of the cranio-cervical plexus, which passes rostrad lateral to the trachea beneath the oral mucosa; it enters the muscle about the level of the larynx.

C. M. Geniotrachealis (GnTr). This muscle is the same size, shape, and has the same general proportions as the genioglossus. It arises from the medial surface of the mandible, and is closely applied to the dorso-lateral surface of the genioglossus. It inserts into the ventral, lateral, and dorso-lateral surfaces of the first dozen or so tracheal rings. It is innervated near its insertion by a branch of the anterior division of the cranio-cervical plexus.

D. M. Hyotrachealis (HyTr). This retractor of the larynx is a narrow, extremely thin muscle which arises from the lateral edge of the ceratohyal immediately caudal to the posterior end of the hyoid origin of the M. neuro-costo-mandibularis. The hyotrachealis passes antero-dorsally as it turns around the sides of the tongue and trachea, and inserts on the lateral aspect of the cricoid cartilage. It crosses the insertion of the geniotrachealis dorsally. The hyotrachealis is innervated by the anterior division of the cranio-cervical plexus; a thin nerve filament branches off the main trunk and enters the muscle near its origin. The hyotrachealis lies directly beneath the mucosa throughout much of its length.

Group Two: Cervical Musculature
(Figs. 18-20, 25-27)

Of the six muscles included in this section, only two (viz. M. neuro-costo-mandibularis and cervico-quadratus) are of importance in the deglutitional mechanism. The other four are included here in order to correlate the data on the trunk musculature of snakes with that of the head region, and to clarify the muscle relationships in the so-called neck region.

A. M. costocutaneus superior (CCS). The muscle bundles originate from the lateral surface of the rib cage, forming together a continuous muscular column ventro-lateral to the M. retractor costae bicepe. The fibers pass latero-caudad and insert into the integument a short distance from the lateral edge of the gastrosteges. The muscle is innervated by the ventral division of the spinal nerves.

B. M. costocutaneus inferior (CCI). The origin is from the lateral surface of the ends of the ribs. The muscle passes as discrete bundles to insert on the end of each gastrostege. The fibers run in a cranio-ventrad direction, beginning from the seventh or eighth rib, and inserting as far rostrad as the fourth gastrostege. At its origin the most rostral muscle bundle is in close approximation to the posterior border of the costal head of the M. neuro-costo-mandibularis; however these muscles are separated by a definite space; furthermore, the neuro-costo-mandibularis takes origin from much of the lateral surface of the rib cage as well as from the tips of the costae themselves. The nerve supply to the M. costocutaneus inferior is via the ventral division of the spinal nerves.

C. M. neuro-costo-mandibularis. This muscle is well-developed and extends over a large part of the throat and neck region. It has three heads of origin which combine to insert by a common aponeurosis on the ventro-lateral surface of the mandible.

Pars vertebralis (NCM, v). The vertebral head has an extensive aponeurosis of origin from the mid-dorsal line caudal to the posterior border of the M. cervico-mandibularis, and from the superficial fascia of the MM. spinalis, semispinalis, and retractor costae biceps. The fibers converge as they swing ventro-lateral between the posterior end of the mandible and the first full-length rib (vertebra 5), at which point the ventral division of spinal nerves 3-4 enter its deep surface. The muscle lies immediately beneath the M. constrictor colli, from which it is readily separated since its fibers cross the latter muscle almost at right angles.

Pars costalis (NCM, c). The costal head originates from the ends of the first several full-length ribs and from the muscles which join the adjacent ends of the costae (M. intercartilaginosus of Hoesner, '35). The superficial and deep portions of the muscle, as described in Thamnophis by Cowan & Rick ('51) could not be identified in Elaphe. The fibers converge somewhat as they pass ventro-rostrad to join the vertebral part of the muscle at the level of the posterticular process of the mandible; however the costal part of the muscle remains postero-ventrad to the vertebral portion.

At about the level of the quadrato-mandibular articulation both the vertebral and costal heads lie side by side in the horizontal plane, with the vertebral portion lateral to the costal. A transverse muscle inscription

occurs at this point, and marks the insertion into the common muscle mass of a small slip of fibers which originates from the gastrostege insertion of the most rostral group of the inferior costocutaneus muscle. This slip of muscle is short, and passes dorso-rostrad to insert into the superficial side of the inscription. The fibers of the vertebral and costal portions of the M. neuro-costo-mandibularis continue rostrad from the inscription to their common insertion on the ventro-lateral surface of the mandible anterior to the mandibular attachment of the intermandibularis posterior, pars posterior and anterior. The muscle ends in a wide aponeurosis which wraps around the ventral edge of the mandible.

Pars hyoidea (NCM, h). The hyoid head of the neuro-costo-mandibularis has a somewhat different course. It originates as an aponeurosis on the ventral midline dorsal to the gastrosteges from the basihyal caudal to about the level of the twelfth gastrostege. The muscles from opposite sides of the body are joined at the mid-ventral origin, but diverge as they split to enclose the median and anterior thirds of the hyoid cornua from which most of the muscle fibers arise. In cross-section the entire structure forms a triangle with the aponeuroses and paired hyoglossal muscles composing the sides, and the raphe and paired ceratohyals the edges. In sagittal view the structure appears as a horizontal pyramid, with the apex at the basihyal where the cornua and raphe meet at a common point. From the cornua of the hyoid the muscle fibers of the pars hyoidea continue rostrad in a common plane with the fused vertebral and costal heads, the whole being joined together in a common fascial sheath. The hyoid head thus forms the rostro-medial portion of the

neuro-costo-mandibular muscle. Like the costal head it is innervated by numerous and variably arranged branches from the cranio-cervical plexus which enter the muscle in the region of the previously-mentioned inscription. The insertion continues over the intermandibular articulation onto the proximal two-thirds of the ventro-lateral surface of the dentary bone.

Although the three heads of the neuro-costo-mandibular are joined at the insertion, the fibers of each component are distinct and can be rather easily separated from each other by sharp dissection.

D. M. cervico-quadratus (CvQ). This muscle originates from the skin of the dorso-lateral neck region superficial to the anterior edge of the vertebral portion of the neuro-costo-mandibularis. It passes antero-dorsad to insert by a tendon into the postero-lateral edge of the proximal end of the quadrate bone, crossing deep to the cervico-mandibularis muscle. It is innervated by several short twigs from the fused spinal nerves 3-4.

E. M. transversus abdominis (TVA). This is a very thin muscle which originates from the inner surface of the rib cage by an extensive aponeurosis, and passes almost directly ventro-mediad in close association with the pharyngeal wall. The insertion is in the mid-ventral line immediately lateral to the origin of the hyoid head of the M. neuro-costo-mandibularis. The rostral edge of the muscle lies at about the level of the first full-length rib. Innervation is by the ventral divisions of the spinal nerves.

F. M. obliquus abdominis internus (OblI). The muscle lies immediately superficial to the former; it has a similar origin, insertion, innervation, and extends over a similar area. It differs only in that the fibers

pass somewhat more craniad, rather than remaining in the transverse plane of the body. Like the transversus abdominis it is extremely thin throughout. It may be noted that these two muscles separate the hyoid head of the M. neuro-costo-mandibularis from the costal head in the posterior hyoid region.

Part Four: Cranio-vertebral Musculature
(Figs. 13, 14, 15, 27)

The MM. spinalis and semispinalis lie superficially on either side of the spinous processes of the vertebrae. Their origin and general pattern are as indicated by Mosauer ('35). In the cranial region the combined muscles (together with the cranial portions of the M. longissimus dorsi) insert on the supraoccipital and dorsal halves of the exoccipital bones caudal to the prominent supraoccipital crest. In this general region they are covered by the M. constrictor colli superficially and the MM. cervico-mandibularis and neuro-costo-mandibularis, vertebral head, beneath. The spinalis and semispinalis muscle masses are the main dorsi-flexors of the cranial component, and are of importance in increasing the size of the gape. Together with the M. retractor costae biceps they aid in turning the head region latemad, also an important function in the swallowing process. All three muscles are innervated by the dorsal division of the spinal nerves.

The M. retractor costae biceps lies ventro-lateral to the M. semi-spinalis, and originates cranially on the mid-lateral and ventro-lateral portion of the exoccipital bone, at which point a prominent osseous process extends latemad. This paroccipital process also serves as the point of attach-

ment for the lateral head of the M. transversohypapophyseus. The retractor costae biceps functions as a lateral flexor of the cranium.

The M. transversohypapophyseus forms a bulky muscle mass on the ventral surface of the vertebral column. Its fibers originate from the transverse processes and pass craniad to insert on the hypapophyses of the vertebrae. In the cranial region the muscle bundles divide into three main groups. The fibers from the ventral surface near the midline run directly rostrad to insert on a prominent tubercle of the basioccipital bone. The greater portion of the transversohypapophyseus swings latered at the level of vertebrae 3-4; this dorsal head inserts over a wide area of the cranium from the paroccipital process mediad to the midline, converging somewhat and covering the entire basioccipital bone except the condyle. The small lateral head originates between the ventral and dorsal heads and passes antero-latered to insert into the pareccipital process ventral to the insertion of the M. retractor costae biceps. All three heads of the transversohypapophyseus act as the chief ventral flexor of the cranium on the vertebral column; the head inserting on the paroccipital process may assist the epaxial musculature in lateral flexion of the cranium. The muscle is supplied by the ventral division of the spinal nerves.

It may be remarked here that all of the axial muscles described by Mosauer ('35) as occurring in colubrids (including Elaphe vulpina) have been identified by the present investigator in Elaphe obsoleta quadrivittata. Only those which play a part in the swallowing process, however, are discussed in the present paper.

CHAPTER V

DISCUSSION AND CONCLUSIONS

Section One: The Functional Anatomy of Deglutition

In the two previous sections the morphology of the individual bones, ligaments, and muscles of the cranial region has been described in detail. Data of this sort, however, is of little significance unless it is analyzed in relation to the part each of these elements plays in the general overall mechanism of deglutition. It is the purpose of the present chapter to correlate the various features of the cranial osteology, arthrology, and myology from the standpoint of function. Expressed sequentially these activities then present a description of the swallowing process as it actually occurs.

Certain general aspects of ophidian anatomy require special mention here, since they serve as prerequisites for understanding the type of swallowing that occurs in snakes. Details of some of these features will be developed later in the chapter.

Of major importance is the complete independence of movement between the two halves of the lower jaw; that is, each mandible acts independently of the other at any given stage in the swallowing process. Correlated with this are several other features. These include distant suspension of the mandibles from the skull via the squamosal and quadrate bones, both of which are highly

movable. A complete lack of a mental symphasis or of ligamentous connections between the tips of the dentary bones occurs in Elaphe and makes possible the independent action of the mandibles as described above. The intramandibular joint, while of importance in the ophidian mode of deglutition, is not found only in snakes, but occurs in some other reptiles as well. Lastly, the highly distensible soft anatomy of the throat and intermandibular region not only allows swallowing of large prey, but makes possible highly-developed movement of one mandible while the other is fixed in position to hold the prey.

Also of significance in understanding the general mode of swallowing in ophidians is the almost complete functional independence of each palato-maxillary arch. These paired arches are connected functionally only via the common nasal component and the palato-vomerine ligaments. In Elaphe all traces of a pterygo-basisphenoid articulation have been lost, kinetism being consequently well developed. The maxillae likewise are extremely movable, having lost all osseous connections with the other bones in the premaxillary, palatal, prefrontal, and postorbital regions.

Thus it can be readily appreciated why most investigators have analyzed the ophidian mode of swallowing on the basis of a four-phase cycle: viz. independent and sequential movement of the two mandibles and the two palato-maxillary arches. As will be shown, however, this hypothesis is not entirely valid. A study of the ligamentous connections, together with direct observation of the swallowing process and analysis of cinefluorographic film, indicates that a two-phase cycle is employed. That is, the mandible together with the ipsilateral palato-maxillary arch is moved, while the contralateral

elements remain fixed to hold the prey; the two sides of the head then revers actions, forming the two-phase cycle. An appreciation of this basic princip is of cardinal importance in understanding the detailed process of deglutitio in snakes.

Other anatomical features of lesser significance afford some explanation of why the swallowing of large prey is possible, though they directly contribute nothing toward explaining the mode in which this is accomplished. Thus, the lack of pectoral appendages, sternum, or sternal ribs, makes possible great expansion of the soft anatomy in the throat and ventral thoracic region. The reduction and elongation of the hyoid apparatus, together with its lack of osseous or ligamentous attachment to the rest of the skeleton, also aids in permitting distensibility of the anterior esophageal region. Modification in the respiratory system is necessitated by the mode of feeding in snakes. Thus the left lung is reduced and almost lost in most snakes, in keeping with the general elongation of the body and viscera. The glottis lies far forward between the dentary bones, thus allowing the snake to breath while the prey is in the posterior jaw region; a well-developed pair of tracheal protracting muscles permits the trachea to be thrust almost to the rostral end of the head, thus further increasing the approach to normal respiration even during the often-times slow process of deglutition. Finally it may be noted that the skin of the snake is not only loosely attached to the underlying structures, but of itself is highly distensible owing to the arrangement of the scales and the extensive cutaneous conjunctiva. Without skin of this type, the internal skeletal and visceral modifications would be of little advantage in swallowing large prey.

Of general interest also is the method in which members of the genus Elaphe capture their prey. These snakes do not strike from a coil; generally they draw the body up in an S-shaped curve anteriorly just before striking. The strike itself is very rapid and often almost too fast to see. Living prey is usually grasped by the head, but this is by no means always the case. The head approach ordinarily results from the fact that the prey is facing its attacker; a hind-leg or mid-body approach often follows an attempt to escape, and on several occasions the writer has observed the snake grasp only the tail in its mouth. The prey, if not too large, is swallowed from either head or tail end, depending upon which is nearer the location of the initial strike. At the instant of strike the snake grasps the prey and pulls its own head back to the region of the coils. The head is quickly thrown to one side while the snake rotates its body in such a way as to bring several coils around the body of its victim. Elaphe does not "throw its coils" around the prey, as sometimes described in the literature; however if the prey continues to struggle the snake may use a part of its body to press it against the substrate. After breathing has ceased, the snake releases its initial grip and loosens the coils somewhat. If the strike was in the head or tail region, swallowing commences at once; if in the mid-body region the snake grasps the prey anew at the most convenient end. As swallowing progresses, Elaphe gradually pulls the prey out of the coils, thus seeming to stretch it out. It was never noted that Elaphe pushed the prey into its mouth by pressure against the substrate or a coil (as does Dasypeltis in swallowing an egg); on the contrary, it often raises its head and neck region eight to ten inches

above the substrate, especially during the last stages of ingestion.

During the deglutitional process, the two-phase cycle mentioned above always occurs. Even with very small prey all the complicated cranial movements were noted. If the prey is large, however, or if difficulty is encountered in passing the jaws over the pelvic or pectoral girdles, the side-to-side alternation in movement may be interrupted temporarily until the snake has obtained a satisfactory position from which to continue. Even after the body of the prey has passed the cranial region all the regular jaw actions continue until the head and neck region return to their normal size.

The distance to which the prey is forced into the mouth at the initial strike varies with the size and the part of the body first encountered. In any case, the second or third bite is usually maximal; that is, the snake forces its jaws over the prey as far as possible. If after the first four or five alternate jaw action sequences little progress is made, the snake may withdraw its head and begin anew at a more favorable location --either the head or tail end, depending on which is more convenient.

The time required to swallow the prey varies with its relative size and general shape; the smaller in maximum diameter, the more rapid the swallowing process. A one-third grown mouse might take thirty seconds, whereas a full-grown mouse would require several minutes after the struggling had ceased; with a specimen too small to constrict in the coils, the jaw actions begin immediately, even while the prey continues its efforts to escape.

It has often been noted that the swallowing of the first mouse (or other prey) stimulates the appetite of the snake, which then immediately be-

gins to move about searching for more. On the other hand, if the snake is not hungry the moving prey serves merely as an annoyance which the snake seeks to escape as readily as possible.

If non-living prey is offered, the snake swallows it in the manner described. Constriction in the coils does not occur in these instances.

It may be noted here that there are no essential differences in jaw movement during the entire swallowing process: beginning, middle, or end all show the same basic pattern of action. However in the descriptions that follow it is assumed for uniformity that the prey is about one-third of the way into the mouth, at which time the jaw structures are separated almost maximally.

In the analysis of the deglutitional process which follows, several commonly-used terms are employed in a somewhat specialized sense. By opening of the mouth is meant increasing the distance between the teeth of the upper and lower jaws on the same side of the head; closing of the mouth is the opposite action. Hence a snake may actually have its mouth open and closed at the same time, even while in the process of swallowing a large food mass; that is, during deglutition one side of the mouth is open while the other side is closed. Elevation-depression, abduction-adduction, protraction-retraction, all retain their usual meanings. The direction of rotation refers to the direction (lateral or medial) in which the tips of the teeth move in the transverse plane. The teeth are said to be engaged when they are driven into the surface of the prey; disengagement is the opposite action.

Part One: The Functional Components

In the previous chapter the skull of Elaphe was described on the basis of its seven functional components: axial, cranial, nasal, palato-

maxillary, squamosal-quadrate, mandibular, and hyoid. Of these the first and last are of secondary importance from the functional standpoint of deglutition in snakes. The cranial component serves as the locus of reference from which the jaw actions are described. The nasal component is the functional intermediary between the cranial component and the paired palato-maxillary arches. The mandibular and closely-related squamosal-quadrate components complete the functional series. It may be recalled that the mandibular, palato-maxillary, and squamosal-quadrate components are all paired functional units, relatively independent of the actions of the same components on the opposite side of the head.

In the pages that follow, each of the dentiferous bones is discussed in turn during opening and then during closing of the mouth. The other cranial structures involved in deglutition are treated in their appropriate place under the main headings: pterygoid, palatine, maxillary, and mandibular actions. It is to be understood, of course, that the actions of all the bones of the head are closely interrelated and that the divisions are only for the purpose of analyzing the smoothly coordinated functional process of deglutition.

Part Two: Opening of the Mouth

During opening of the mouth there are three general actions: drawing the dentiferous bones away from the surface of the prey, thus disengaging the teeth; separating these bones further from each other, thus enlarging the size of the mouth opening; and carrying these bones further over the surface of the prey in order to re-engage the teeth and thus pull the prey caudad.

Hence elevation of the upper jaw and depression of the lower jaw, abduction, lateral rotation, and protraction are the chief actions of the dentiferous bones.

A. Actions of the Pterygoid Bone (Figs. 28-30, 32-35). The actions of the pterygoid bone during opening of the mouth are rather complex, owing to the kinetism of the ophidian skull. The bone itself has a longitudinal axis of rotation which passes through the anterior two thirds of the bone immediately dorsal to the tooth row, a transverse axis passing through its articulation with the palatine bone, and a vertical axis crossing the other two at right angles. The muscle attachments lie lateral to the longitudinal axis for the most part on the dorsal and ventral surfaces of the vane and shaft.

The pterygoid bone is protracted by the action of the M. protractor ossis pterygoidei, the fibers of which pass from the dorsal surface of the vane in a dorso-medial direction to their origin on the basisphenoid. Since there is no pterygo-basisphenoid articulation in Elaphe, the effect of contraction of this muscle varies accordingly to the position of the pterygoid bone, which is in turn dependent on the concurrent action of the M. levator ossis pterygoidei which is acting at the same time; thus when the latter muscle contracts the adducting effect of the protractor is minimized. The general result of contraction of the protractor is a rostral movement of the pterygoid bone which thus disengages the caudally curved teeth. Owing to other features yet to be mentioned, the overall result however is not a simple rostral thrust of the bone in the horizontal plane (vd. infra).

Together with protraction of the pterygoid bone occurs a definite elevation-abduction action, brought about by contraction of the M. levator ossis pterygoidei. This muscle inserts on the dorsal surface of the vane and shaft lateral and anterior to the insertion of the pterygoid protractor. However the fibers of the levator do not run mediad (as do those of the protractor), but dorso-laterad towards their origin on the ventro-lateral surface of the os parietale. Hence contraction of this muscle adducts as well as elevates the pterygoid bone as a whole, as has been noted by direct observation, cinefluorograph analysis, and electrical stimulation studies. Both the protractor and levator work together; since the former pulls dorso-medially and the latter dorso-laterally, the net effect is essentially direct elevation of the pterygoid bone. At the same time, the levator abducts and the protractor protracts. Thus when the two muscles contract the pterygoid bone moves in a dorso-rostro-lateral direction.

The protracting effect of the M. protractor ossis pterygoidei would theoretically pull the bone rostrad, since the muscle fibers are directed more dorso-rostrad than dorso-mediad. However anteriorly the end of the pterygoid bone abuts against the caudal end of the palatine bone at the palatine-pterygoid saddle joint. Since the palatine bone is connected via the palato-vomerine ligament to the non-protractile nasal component, protraction of the pterygoid bone directly rostrad is prevented. Instead the palatine bone rotates in the horizontal plane around the vertical axis through the palato-vomerine ligament, thus swinging the posterior end of the palatine bone laterad and with it the attached anterior end of the os pterygoideum. Since the leva-

tor of the pterygoid bone is contracting at the same time, and pulling in a dorso-lateral direction, the net effect is a dorso-rostro-lateral movement, as has been described. Thus the palatine bone serves as a radius which describes an arc around which the anterior end of the pterygoid bone moves; the rotational axes are at the palato-vomerine ligament and the pterygo-palatine articulation.

The above actions also rotate the pterygoid teeth laterally due to the action of the M. levator ossis pterygoidei which pulls dorso-latered since most of its fibers insert dorsally on the vane lateral to the axis of longitudinal rotation which lies dorsal to the tooth row. This rotating effect is aided by the postfronto-maxillary ligament which prevents the caudal end of the maxilla from being abducted directly laterad. Instead the lateral thrust of the mid-section of the pterygoid bone, via the os ectopterygoideum, rotates the maxilla laterally around the postfrontal bone and swings the proximal end of the ectopterygoid bone ventrad. Since the pterygo-ectopterygoid articulation is flat in the horizontal plane, and has no sagittal axis of its own, the pterygoid bone of necessity is rotated around its longitudinal axis during abduction, thus laterally rotating the teeth. The net result of these three concomitant actions is disengagement of the caudally curved pterygoid teeth (pretraction), lateral rotation of the teeth during rotation of the bone as a whole, and abduction of the entire pterygoid bone.

Of secondary importance is the abduction of the opposite side of the head, due to contraction of the contralateral M. retractor costae biceps and the lateral head of the M. transversohypapophyseus; this thrusts the ipsilat-

eral side of the head further over the surface of the prey and materially aids the protracting effect with reference to the prey.

It might reasonably be assumed that during these actions the tooth row of the pterygoid bone remains parallel to the base of the brain case. That this is not what actually occurs will be appreciated after the analysis of the actions of the os palatinum (vd. infra).

Though the pterygoid bone cannot ordinarily be observed in the living snake during swallowing, its action may be seen during study of the cinefluorograph films. Furthermore, the rotating actions and abduction can at times be seen during the swallowing of small prey, and near the end of the swallowing of large prey when the last few centimeters of the latter are still in the region of the occipital condyle. At this time the mouth is still agape and the bones continue to trace their characteristic pattern of movement even though the prey is no longer in the immediate vicinity. It is on evidence such as this, together with extensive dissections, that the functional analysis of the pterygoid actions is based.

B. Actions of the Palatine Bone (Figs. 31-35). The movements of the os palatinum involve several axes of rotation. The pterygoid and palatine bones articulate at a saddle joint with vertical and transverse rotational axes. The palatine bone itself articulates with the nasal component via the palato-vomerine ligament which inserts on the dorsal surface of its anterior end; it articulates with the prefrontal bone via the prefronto-palatine ligament which lies in the same plane as does the palato-vomerine ligament further rostrad. Both these ligaments are loose enough to allow movement around ver-

tical and transverse axes at least to some extent, and around two parallel longitudinal axes movement is quite extensive. The first (or ventral) longitudinal axis is located at the attachment of the two ligaments to the dorsal surface of the palatine bone, rather than in the center of the shaft of the bone; thus rotation tends to roll the bone dorso-laterally or dorso-medially to a slight extent. The second (or dorsal) longitudinal axis is located at the attachment of the ligaments to the vomer and prefrontal bones; around this axis both of the ligaments and the palatine bone itself rotate as a unit. In effect, the palatine bone rotates around the circumferential end of a radius (the taut ligament), which in turn rotates around its own central axis (the attachment of the ligament to the vomer and prefrontal bone). Both axes remain parallel to each other, as has been noted.

Closely related to the palatine actions are several movements possible at the fronto-nasal articulation. The nasal component is able to be elevated and depressed around the transverse axis (Cf. Chapter IV), and due to the looseness of the connection a slight mid-longitudinal rotation is also possible.

Thus abduction of the pterygoid bone rotates the caudal end of the os palatinum laterad around the vertical axis of the pterygo-palatine articulation and the anterior vertical axis of the palatine bone as well. This places the longitudinal axes of the palatine bone at an oblique horizontal angle extending caudo-laterad from its anterior end.

Protraction of the pterygoid bone, however, does not protract the os palatinum, since the latter is connected to the non-protractile nasal

component. Thus the protraction not only rotates the palatine bone around its vertical axes, but around the fronto-nasal transverse axis and the pterygo-palatine transverse axis. The rostrally-directed force of the pterygoid bone rotates the nasal complex upward around the fronto-nasal axis. Since this same force is applied to the vomer at a point latero-ventral to the mid-longitudinal axis of rotation of the fronto-nasal articulation, the nasal component is also rotated laterally to a slight extent when the pterygoid bone is protracted. This elevation of the nasal complex carries the anterior end of the palatine bone with it, thus depressing the posterior end and the attached anterior end of the pterygoid bone.

The overall summary of these palatine and pterygoid actions may be outlined as follows. During opening of the mouth the anterior end of the palatine and posterior end of the pterygoid bones are elevated. The entire pterygoid bone is abducted, and with it the posterior end of the os palatinum, thus forming the horizontal oblique palato-pterygoid angle (Figure 35). At the same time the region of this articulation is depressed, forming the vertical oblique angle (Figure 33). These combined actions effectively increase the space between the two pterygo-maxillary components thus allowing enlargement of the mouth cavity.

It may be noted that the depression of the pterygo-palatine articulation is relative to the base of the cranium, not to the surface of the prey. Since the cranium is being elevated (contraction of the ipsilateral Mm. spinalis and semispinalis) at the same time as the articular area is being depressed, the net result is that the shaft of the pterygoid bone remains par-

allel to the surface of the prey. It might be thought even this relative depression of the region of the pterygo-palatine articulation would hardly be effective in increasing the size of the gape. However if it were not for the transverse axis of rotation at this point the elevation of the nasal component would compress the ocular structures between the cranium and the dorsal surface of the os palatinum. Furthermore, even if the pterygoid bone is not drawn coppletely free from the surface of the prey, the sharply recurved teeth are able to slide rostrad as the bone is protracted.

In conjunction with the actions described in the preceding paragraphs, the palatine bone is also rotated laterally. This occurs in two ways. First, the pterygo-palatine saddle articulation does not allow independent rotation of one or the other of the two bones around a longitudinal axis. Hence lateral rotation of the pterygoid bone rotates the os palatinum along with it, and vice-versa. Secondly, during opening of the mouth the maxilla is also elevated, abducted, and laterally rotated (vd. infra). This maxillary action elevates and rotates the palatine process of the maxilla laterad, and thereby pulls the palato-maxillary ligament attached to it in a dorso-lateral direction. Since this ligament is attached to it in a dorsotrally directed maxillary process of the os palatinum, these actions of the maxilla laterally rotate the palatine bone around its two longitudinal axes. The palatine bone itself cannot be elevated to any great extent in this area because of the prefrontal bone, beneath the ventral surface of which slides the palato-maxillary ligament. Hence dorso-lateral pull on the palato-maxillary ligament exerts force chiefly in the lateral direction.

Abduction of the palatine bone in this area, on the other hand, is limited by the prefronto-palatine ligament. Since the maxillary process of the palatine bone and the palatine process of the maxilla are curved ventrad slightly when the teeth are in the vertical plane, the maxillary actions described above have but one effect on the palatine bone, viz. lateral rotation.

The actions of the os palatinum are here described chiefly from direct observation of the swallowing process as viewed from the ventro-anterior aspect. Elevation and rotation of the nasal segment may be observed from the dorsal aspect since there appears a slight fold in the dorsal scalation directly over the fronto-nasal ligament during opening of the mouth; this is apparent only during the swallowing of large prey. The depression of the region of the pterygo-palatine articulation can be seen by direct observation and is especially noticable in lateral cinefluorographs. The palatine bone is much more easily observed than is the os pterygoideum, since during opening of the gape it is slanted obliquely caudo-ventrad (as well as caudo-laterad) and hence is not in contact with the surface of the prey. During direct observation from a ventro-anterior position the rotating actions of the palatine bone are especially apparent. The limiting actions of the numerous ligaments are, of course, inferred from an analysis of the actions of the bones to which they are attached.

C. Actions of the Maxilla (Figs. 29-35). The movements of the maxilla during opening of the mouth are not nearly as complicated as those of the os palatinum. However the maxilla does undergo much more movement than in other reptilian forms in which it is bound to the other bones of the area

more or less firmly (Cf. Section Two of this chapter). In Elaphe the chief action during opening of the mouth is a combination of abduction, elevation, and lateral rotation.

As in the case of the os palatinum, there are two longitudinal axes of rotation. The first (or ventral) axis passes through the attachment of the prefronto- and postfronto-maxillary ligaments to the dorso-lateral surface of the shaft of the bone. The second (or dorsal) axis passes parallel to the first at the connection of these two ligaments to the prefrontal and postfrontal bones. The maxilla rotates around the taut ligaments at the first axis; both the maxilla and the ligaments rotate around the prefrontal and postfrontal bones at the second axis.

When the mouth is opened the protraction and abduction of the pterygoid bone thrusts the ectopterygoid bone laterad. However the region of the ectopterygoid-maxillary articulation cannot be abducted directly latered because of the attachments of the postfrontal-maxillary ligament. The direction of the lateral force of the ectopterygoid bone is changed by the ligament so that the caudal end of the maxilla is rotated dorso-laterad (elevated and abducted) rather than abducted directly. These actions take place around both longitudinal axes of the maxilla. These actions take place around axes which are parallel to each other, however, and thus the maxilla is elevated, abducted, and laterally rotated all at the same time. This overall effect may be noted by direct observation from either the lateral or the ventral aspect; the large superior labial scutes also move outward and upward in relation to the more firmly fixed scales immediately dorsal to them. Cinefluorograph

studies show the general elevation of the maxilla; direct observation provides information regarding the abduction and lateral rotating effects.

It might be thought that the premaxillo-maxillary and the septo-maxillo-maxillary ligaments assist in elevating the maxilla during opening of the mouth, since at this time the nasal component is also being elevated. This, however, is questionable. The caudal attachment of both of these ligaments is on the palatine process of the maxilla which is being rotated ventro-latered around the ventral longitudinal axis of the maxilla, while at the same time it is being elevated with the maxilla as the latter rotates at the attachment of the ligament to the prefrontal bone. Thus the insertion area of the ligaments on the palatine process of the maxilla is moving in a lateral direction chiefly, not undergoing elevation.

Furthermore the attachments of the premaxillo- and septomaxillo-maxillary ligaments to the nasal component are such that the latter cannot be abducted, since there is no rotation of the nasal component around a vertical axis through the fronto-nasal articulation. Hence the two ligaments serve rather as check ligaments against excessive lateral rotation of the maxilla. Thus, though the nasal component is being elevated slightly, the maxilla is also being elevated-abducted-rotated at the same time; the concomitant elevation of the two retains the two ligaments close to the horizontal plane with reference to the cranium. It appears from the evidence that the premaxillo- and septomaxillo-maxillary ligaments are employed rather as check ligaments against excessive lateral rotation than as elevators of the maxilla.

That there is need for check ligaments may be inferred from analysis

of the strong protracting effects of the M. protractor ossis pterygoidei, as noted in electrical stimulation studies. Contraction of this muscle and of the M. levator ossis pterygoidei thrusts the caudal end of the maxilla laterad and the proximal end of the ectopterygoid bone antero-ventrad. Thus the maxilla is laterally rotated with great force, against which the two ligaments serve as a check.

This strong lateral thrust of the ectopterygoid bone against the caudal end of the maxilla might conceivably flex the bone in the orbital region, since the maxilla is flattened in the vertical plane and rather thin in this area. To prevent this flexion is the function of the intramaxillary ligament. This strongly-developed ligament stretches between the palato- and ectopterygo-maxillary processes of the maxilla, and materially aids in prevention of flexion of the thin maxilla when force is applied to its caudal end; it thus serves as does an architectural stay.

During opening of the mouth the maxilla may undergo a slight amount of protraction because of the length of the postfronto- and prefronto-maxillary ligaments, which allows the maxilla to swing rostrad slightly in an arc. Excessive protraction of the maxilla would tend to compress the ventral ocular structures between the postfronto-maxillary ligament and the prefrontal bone, though the slight amount of movement possible at the prefronto-frontal articulation would tend to offset this. In any case, it may sometimes be noted that the eye is distorted slightly during swallowing of large prey. It appears that the protraction of the maxilla in reference to the prey is in reality chiefly due to the forward thrust of the ipsilateral head region as a whole

which occurs when the contralateral epaxial musculature (including the M. retractor costae biceps) contracts.

D. Actions of the Mandible (Figs. 28, 29, 33, 34). There are many axes of rotation involved in movements of the mandible. A transverse axis passes through the squamosal-parietal articulation. A longitudinal axis passes through the body of the squamosal itself, allowing the bone to rotate slightly over the surface of the underlying ossa prooticum and parietale. The squamosal and quadrate bones are articulated in such a way that only a transverse axis occurs at their junction. The quadrate and mandible articulate in a saddle joint with longitudinal and transverse axes of rotation. And the intramandibular articulation has only a vertical axis. All of these axes of rotation give the dentary bone (which bears the teeth) great freedom of movement and allows it to move in any direction. It may be noted here that in this and the following paragraphs the axes of rotation are described as if the mouth were opened only slightly, as in Figure 34. During swallowing of large prey these axes vary in spatial direction; thus the vertical intramandibular articulation may become almost longitudinal, as in Figure 33.

During opening of the mouth the dentary bone is depressed, abducted, laterally rotated, and protracted. All of these actions serve to disengage the teeth and draw them away from the surface of the prey, and then to carry them forward where they are in position to grasp the prey anew and pull it further into the mouth.

Depression of the dentary bone occurs in three ways, all of which act together. First, contraction of the M. cervico-mandibularis; second,

contraction of the M. occipito-quadrato-mandibularis; third, contraction of the MM. neuro-costo-mandibularis, and the anterior and posterior intermandibulares.

The fibers of the M. cervico-quadratus insert into the proximal end of the quadrate bone and are directed ventro-caudad to their origin in the skin of the neck region. When they contract they depress the region of the quadrato-squamosal articulation, rotation occurring around both transverse axes of the squamosal bone. This action thrusts the quadrate bone and the attached musculature and mandible ventrad, thus increasing the curvature of the arc formed by the squamosal, quadrate, and mandibular bones. Depression here is with reference to the cranium.

The M. occipito-quadrato-mandibularis passes from its origin on the posterior surface of the quadrate bone to insert on the dorsal surface of the mandibular postarticular process. Contraction of this muscle elevates the postarticular process and thereby depresses the dentary bone with reference to the os quadratum. The rotation occurs around the transverse axis of the quadrato-mandibular joint.

The M. neuro-costo-mandibularis is not an effective depressor of the mandible when the head is in the normal resting position, since the muscle fibers are mostly in the same horizontal plane of the mandible at this time. However during swallowing the intermandibular region is stretched medio-ventrad from the mandible by the bulk of the prey being ingested; the muscle fibers therefore also are directed medio-ventrad from the mandible. Furthermore, during swallowing the mandible does not remain parallel to the cranium,

but is depressed by the M. occipito-quadrato-mandibularis until it is almost at right angles (Fig. 33). In this latter position the M. neuro-costo-mandibularis is in effective position to depress the mandible (as well as to laterally rotate it, vd. infra).

Evidence for the actions described in the above paragraphs is had chiefly from the cineflucrograph studies. The relations of the squamosal, quadrate, and mandibular bones during various stages of the swallowing process can only be brought about by the contraction of the MM. cervico-quadratus and occipito-quadrato-mandibularis, as described. The synergistic depressing action of the M. neuro-costo-mandibularis is inferred. That this muscle is not the sole depressor of the mandible on the quadrate bone is evident from the fact that the mouth can be opened even when there is nothing in it, as happens at the initial strike or during yawning. At this time the muscle fibers of the M. neuro-costo-mandibularis are not in effective position to depress the mandible with any significant degree of speed.

Lateral rotation of the dentary bone takes place around the longitudinal axis of the mandible, which passes through the shaft of the bone. At least some (and it is assumed all) of the following muscles take part in this action: MM. neuro-costo-mandibularis and all divisions of the anterior and posterior intermandibulares. All of these muscles insert on the ventro-lateral surface oft he mandible, though the anterior part of the posterior intermandibular muscle also inserts on the medial surface of the compound bone to a slight extent. In the resting position the fibers of each muscle pass around the ventral surface of the mandible and continue toward the midline in the hor-

izontal plane. However when the mouth is distended by the bulk of the prey, the soft anatomy of the intermandibular region is forced ventro-mediad towards the midline. Thus contraction of these muscles while the mouth is opened tends to rotate the teeth laterad, and hence disengage them from the prey.

When the mouth is distended the M. protractor quadrati is also in a position to rotate the mandibular teeth laterad, as it pulls the ventro-medial surface of the bone dorso-mediad toward its insertion in the ventral occipital region. But there is no direct evidence that this actually occurs.

Contraction of the anterior intermandibular muscle, however, not only rotates the mandible around its longitudinal axis, but flexes the dentary bone mediad around the vertical (or longitudinal, when the mouth is opened) axis of the intermandibular region. This action abducts and laterally rotates those teeth which lie proximal to the intramandibular joint, thus effectively disengaging them, since they point mediad as well as caudad. The teeth distal to the articulation are adducted and rotated laterally; this action disengages the teeth although the shaft of the mandible is adducted against the surface of the prey. However since the teeth are disengaged the shaft of the mandible is still free to slip over the surface of the prey before a new grip is obtained. Furthermore, while the mandibles are maximally depressed during swallowing of the prey, this flexion in the intramandibular region allows the dentary bones to curve themselves around the surface of the (usually) cylindrical prey. This allows the snake to swallow large size prey without putting added strain on the intermandibular region between the dentary bones, as would occur if the anterior ends of the mandibles were as far separated as the proximal

ends. It also keeps the soft anatomy of the throat region in closer proximity to the ventral surface of the prey, thus preventing the latter from working itself free while the mouth is opened and a new grip being obtained. The flexion of the mandible at the intramandibular articulation can best be observed by watching the swallowing process from a position directly anterior to the snake. Lateral rotation (together with mandibular depression) is then easily noted, and the intramandibular flexion can usually be seen.

It may be theorized that the medial flexion of the dentary bone (together with protraction of the mandible as a whole, which occurs at the same time) would tend to thrust the intramandibular region latered to some extent. This abduction of the middle of the mandible would theoretically increase the gape and abduct the posterior mandibular region, if the anterior end of the dentary bone were stabilized against the surface of the prey. However the entire dentary bone is drawn away from the surface of the prey in those instances in which the action of the bone can be observed. Whether this abduction occurs at all times, or at any time, during the swallowing process is a matter for speculation.

Abduction of the mandible as a whole is in most respects a passive action, no muscle being in effective position to abduct the mandible, quadrate, or squamosal bones. However since the prey is swallowed from either end rather than at the bulky mid-body region, the jaws are gradually forced latered as the constantly increasing bulk of the prey is engulfed. Nevertheless, the present investigator has often noted that the oral mucosa at the angle of the jaw is drawn latered from the surface of the prey, and hence the action is more than

merely passive. Perhaps the abduction of the mucosa in this region is brought about by the lateral rotation of the mandible to which it is attached. Again, it would seem in view of the anatomy involved that the abduction-elevation-rotation of the maxilla at this phase of the swallowing process would tend to pull the quadrato-maxillary ligament and attached quadrato-mandibular region somewhat lateral. All of this, however, is merely speculation and no direct evidence is had. Nevertheless the proximal end of the mandible is definitely abducted (rotation occurring around the longitudinal axis of the squamosal bone), and no muscle is in effective position to accomplish the task; therefore it would seem that the action of the quadrato-maxillary ligament is quite likely the correct explanation. The superficial temporal musculature, of course, is in the correct position to abduct the mandible to some extent, but it would also elevate the mandible at the same time--hardly a suitable action to increase the gape.

Protraction of the mandible occurs at the same time as the other mandibular actions previously described, thus carrying the dentary teeth further forward over the surface of the prey. There is no direct mandibular protracting muscle; the bulky adductor mandibulae internus, pars anterior, which has this function in other animals has a different function in snakes, as will be shown (vd. infra). However protraction of the pterygoid bone pulls the caudal end of the mandible forward via the pterygo-mandibular ligament and thus accomplishes the same end. The maxilla is not protracted to any great extent, as has been shown, and hence cannot have any significant protracting effect on the mandible via the strong quadrato-maxillary ligament. Since the ventral

midline is relatively fixed in position by the contralateral intermandibular musculature, the ipsilateral posterior intermandibular musculature could theoretically protract the mandible since the fibers run medio-rostrad from their mandibular attachment. However these fibers run more mediad (and ventrad, when the mouth is open) than rostrad; hence their protracting effect is minimized. What is more, they are much too weak to have the strong protracting effect required in forcing the jaws over the resisting bulk of the prey, as electrical stumulation experiments show. Much of the apparent protraction of the mandible results from the contracting actions of the contralateral ventral axial musculature; this thrusts the ipsilateral head region as a whole further over the surface of the prey.

In summary we may note that the actions described in Part Two effectively accomplishes the three-fold end outlined at the beginning, viz.: drawing the dentiferous bones away from the surface of the prey, thus disengaging the teeth; separating these bones further from each other, thus enlarging the size of the mouth opening; and carrying these bones further over the surface of the prey in order to re-engage the teeth. Direct observation, electrical stimulation studies, and especially the cinefluorographic investigations (together with a thorough analysis of the anatomy of the structures involved) have enabled us to reconstruct the action sequences as they occur during opening of the mouth, and to determine the moving forces for each dentiferous bone. In no case has the evidence made it necessary to speculate concerning the source of an observable action; the small amount of theorizing concerns only the possibility of secondary muscles aiding the main muscles in a synergistic

fashion, as in the case of the lateral rotating effect of the mandible following contraction of the M. protractor ossis quadrati.

It remains now to outline and discuss the mechanisms involved in the opposite actions of the dentiferous bones, i.e., the actions which close the mouth.

Part Three: Closing of the Mouth

The second half of the two-phase ophidian deglutitional cycle is concerned with those actions which close the mouth, or approximate the dentiferous bones of the upper and lower jaws. This second phase, of course, is directly opposed to those movements described in the previous section of this chapter. The same bones, ligaments, and rotational axes are involved; the muscles however are different. Closing of the mouth is directed toward the attainment of three chief ends: drawing of the dentiferous bones closer to the surface of the prey, thus bringing the teeth into position for a renewed grip; drawing of the dentiferous bones closer to each other, thus decreasing the size of the mouth opening; drawing of the bones caudad, thus re-engaging the teeth and holding the prey so that the opposite side of the head can be carried forward over its surface. Hence depression of the upper jaw and elevation of the lower jaw, adduction, medial rotation, and retraction are the chief actions of the bones.

A. Actions of the Pterygoid Bones (Figs. 28-30, 32-35). The axes of rotation of the os pterygoideum are those previously described, viz. the longitudinal through the shaft of the bone dorsad to the tooth row, and vertical and transverse axes at the pterygo-palatine articulation.

Retraction of the pterygoid bone is brought about by several simultaneous actions, of which contraction of the M. cervico-mandibularis and the M. retractor ossis pterygoidei are the most important. The fibers of the former muscle extend rostro-laterally to the level of the quadrato-mandibular articulation where they insert on the lateral surface of the distal end of the quadrate bone; their origin is along the mid-dorsal region of the neck. Contraction of the muscle draws the distal end of the quadrate bone caudad, and with it the pterygoid bone via the pterygo-mandibular ligament. At the same time the M. retractor ossis pterygoidei, the fibers of which pass from the basisphenoid midline rostro-ventrally to the dorsal surface of the medial edge of the os palatinum, contracts and thus restores the shaft of the latter bone to the paresagittal position. The action draws the pterygo-palatine articulation caudad as well as medio-dorsad; rotation takes place around both the transverse and the vertical axis. By this means the pterygoid bone as a whole is retracted, thus engaging the teeth. The effects of the M. cervico-mandibularis are readily noted in an analysis of the cinefluorographs; contraction of the M. retractor ossis pteyygoidei may be seen as the mucosa over the muscle is stretched when the muscle fibers contract.

It may be inferred that several other mechanical features aid in retracting the pterygoid bone as the mouth is closed, although direct evidence is lacking. Contraction of the M. retractor vomeris, which extends from the basisphenoid to the postero-inferior process of the vomer, depresses and somewhat retracts the nasal complex; these combined actions occur as the nasal segment is rotated in an arc around the transverse axis of the fronto-nasal

articulation. The retraction effects of this rotation would tend to thrust the palatine bone (which is attached via the palato-vomerine ligament) in a caudal direction, thus retracting the os pterygoideum. It is evident that the retracting effects of the MM. retractor ossis pterygoidei and retractor vomeris cannot be distinguished; both muscles are contracting simultaneously. Whether the palatine bone is drawing the nasal complex down and back (M. retractor ossis pterygoidei), or the nasal component is thrusting the palatine in this direction (M. retractor vomeris) is unimportant; both most likely occur.

In conjunction with the actions described above, it may be noted, the ipsilateral flexion of the head (contraction of the M. retractor costae biceps and lateral head of the M. transversohypapophyseus) tends to draw the prey caudad in relation to the contralateral side of the head. Although this is not pterygoid retraction sensu stricto, it does have the same ultimate effect on the prey.

Adduction of the os pterygoideum is brought about in close conjunction with retraction; the two occur together and the resultant action is movement of the pterygoid bone in a caudo-medial direction. This serves to compress the prey medially and force it back into the narrower occipital region of the pharynx.

When the mouth is open, the region of the pterygo-palatine articulation is abducted (Fig. 35 and vd. supra). Contraction of the M. retractor ossis pterygoidei increases the angle of the pterygoid and palatine bones to 180°, rotation taking place around both axes of their common articulation.

This brings the anterior end of the pterygoid bone (and posterior end of the os palatinum) toward the midline, i.e., adducts it. The posterior end (vane) of the pterygoid bone is adducted to a lesser extent. However the prey is compressible only to a limited extent; if the posterior jaw region were drawn toward the midline to any great degree it would slow the swallowing process. Since it is the anterior end of the pterygoid bone (which bears the teeth) that is adducted most, the pharyngeal region nearer the occipital condyle is seen to expand constantly during swallowing. When the posterior cranial region is observed from the dorsal aspect, the quadrato-mandibular area thus appears to be expanded as the bulk of the prey is forced caudad by adduction of the pterygo-palatine region.

In conjunction with retraction and adduction, the teeth of the pterygoid bone are rotated medially as well. This is brought about by medial rotation of the palatine bone, the posterior end of which is also being adducted and retracted at the same time. The M. retractor ossis pterygoidei is the chief agent in this action. When the mouth is opened the palatine bone is rotated laterally around its longitudinal axes; this ventrally rotates the dorso-medial edge of the shaft of the bone on which the muscle inserts. When the muscle contracts during closure of the mouth, the fibers pull dorso-medially towards the basisphenoid area of origin, thus rotating the palatine teeth medially and adducting the bone as well. Since the pterygoid and palatine bones are not independently rotated laterally or medially around the longitudinal axis of their common articulation, medial rotation of the os palatinum medially rotates the pterygoid bone as well. This entire action may be observed from

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the rostral aspect during the swallowing of small prey, and can be demonstrated by electrical stimulation methods.

The teeth of the pterygoid bone are also rotated medially by contraction of the M. adductor mandibulae internus, pars posterior. The fibers of this muscle originate on the medial surface of the mandible and pass horizontally to their insertion on the ventral surface of the pterygoid vane. However when the mouth is distended, this muscle curves around the surface of the prey. Thus on contraction it draws the mandible dorso-medially (mandibular elevation and lateral rotation, vd. infra) and depresses the pterygoid vane, rotating the latter bone with its teeth around the longitudinal axis of its shaft.

Finally, the pterygoid bone is rotated medially when the maxilla is depressed-adducted (vd. infra). This maxillary action depresses the caudal end of the maxilla and the attached distal end of the os ectopterygoideum. Since there is no longitudinal axis of rotation at the pterygo-ectopterygoid articulation itself, depression of the distal end of the ectopterygoid bone rotates both bones around the longitudinal axis of the os pterygoideum and thus medially rotates the pterygoid teeth.

Depression of the pterygoid bone is strickly relative, since contraction of the MM. cervico-mandibularis, retractor vomeris, and retractor ossis pterygoidei would tend to draw the bone upward. However during closing of the mouth the entire ipsilateral cranial region is strongly flexed ventrally around the transverse rotational axis of the atlas-occipital articulation; the ipsilateral ventral and medial heads of the M. transversohypapophyseus

with the mandibular elevators originating on the cranium bring about this movement; the M. cervico-mandibularis and the quadrato-maxillary ligament probably assist. Thus the cranial, pterygo-maxillary, and nasal components are depressed with reference to the prey on the ipsilateral side. Hence the pterygoid bone itself is pushed ventrad from above, thus depressing it with reference to the prey.

All these actions of the pterygoid bone tend to a single objective: forcing of the prey medio-caudad into the postcranial esophagus. For this purpose the teeth are re-engaged and drawn caudad in such a way that the prey is literally stuffed into the relatively small esophageal space in the region of the occipital condyle. That the pterygoid bone actually undergoes the complicated actions described there can be no doubt; it can be observed directly during the swallowing of small prey or during the last stages of deglutition of large prey. Cinefluorographic and electrical stimulation studies add corroborative evidence to the data obtained by dissection. Analyses of all this information together thus determines the only possible mode in which the observed actions could occur.

B. Actions of the Palatine Bone (Figs. 29-35). This section may be treated more briefly, since the actions have already been analyzed in some detail during the discussion of the movements of the os pterygoideum. Contraction of the M. retractor ossis pterygoidei draws the os palatinum dorso-caudo-medad; this rotates the bone medially around the vertical axis which passes through the palato-vomerine ligament, dorso-caudad (with the nasal component) around the transverse fronto-nasal axis, and rotates the palatine teeth mediad

around the longitudinal axes of the palatine bone itself. The resultant of all these movements elevates the posterior end of the palatine bone, depresses the anterior end along with the nasal region, retracts the entire bone slightly (together with the nasal segment) aided by the M. retractor vomeris, and rotates the bone medially. The palatine bone is thus in a position to assist the pterygoid bone in forcing the prey back into the occipital region. Direct observation, however, indicates that the palatine bone is much less effective than the pterygoid in accomplishing this end; analysis of the cinefluorograph material and of the tooth marks on recovered prey confirms this statement. However the effects of the palatine bone on controlling the actions of the os pterygoideum in relation to the nasal and cranial components must not be minimized, since the palatine bone serves as a functional connection between these components and the pterygoid bone.

The pterygoid movements brought about by action of the posterior end of the mandible and quadrate, via the quadrato-maxillary ligament, ectopterygoid bone, and pterygo-mandibular ligament, are of course transferred to the palatine bone through the pterygo-palatine articulation. The actions of the pterygoid bone supplement the effects of contraction of the MM. retractor ossis pterygoidei and retractor vomeris which control the palatine bone more directly. To reiterate the former here would only repeat what has already been said in a slightly different connection.

C. Actions of the Maxilla (Figs. 29-35). During closing of the mouth the movements of the maxilla are less complex than are those of the pterygoid and palatine bones; this is due chiefly to the limited number of

rotational axes. As has been noted, there are two longitudinal axes involved in maxillary rotation. The first of these (the ventral) passes through the insertion of the prefronto- and postfronto-maxillary ligaments on the dorso-lateral surface of the bone, as has been described. The second (or dorsal) passes through the attachments of these same ligaments to the prefrontal and postfrontal bones. The maxilla and ligaments rotate around the prefrontal and postfrontal bones at the dorsal axis; the maxillarotates around the taut ligaments themselves at the ventral axis. In effect, the maxilla rotates around the circumferential end of a radius, which in turn rotates around its own central axis; both axes of rotation remain parallel to each other as has been noted.

When the mouth is closed the maxilla is adducted around the dorsal maxillary axis, the bone passing chiefly in a ventro-medial direction. At the same time it rotates medially around the ventral axis, thus rotating the teeth from a lateral to a ventral position with reference to its shaft. Both of these actions occur together and are brought about by the same forces.

The chief agent of movement is the quadrato-maxillary ligament. During contraction of the M. cervico-mandibularis the distal end of the quadrate bone is retracted, as has been described previously. This pulls the ligament, which extends between the distal end of the quadrate bone and the caudal end of the maxilla. Contraction of the cervico-mandibular muscle rotates the quadrate bone caudad around the transverse axis of the quadrato-squamosal articulation, and rotates the quadrate and squamosal bones together caudo-dorsad around the transverse axis of the parietal-squamosal articulation. Since when

the gape is wide the ligament extends dorso-rostrad from the quadrate bone, contraction of the cervico-mandibular muscle pulls the maxilla ventro-caudad. And because the protraction-retraction movements of the maxilla are limited by the prefronto- and postfronto-maxillary ligaments, the chief movement of the maxilla is ventro-medial rotation around the parallel longitudinal axes of this bone. The above movements can be seen by direct observation and cine-fluorograph analysis.

Retraction of the maxilla with reference to the prey does occur, however; this follows contraction of the ipsilateral MM. retractor costae biceps, transversohypapophyseus, and adductor mandibulae internus, pars anterior. On contraction of these muscles the entire maxilla and anterior upper jaw region describes an arc as the cranium rotates around the transverse atlas-occipital axis; thus the maxilla is depressed and retracted with reference to the prey. Other movements brought about by contraction of the M. adductor internus, pars anterior, will be discussed in detail later in the present chapter.

The resultant of the movements described in the previous paragraphs drives the maxillary teeth into the surface of the prey and pulls it caudad. Actually the maxilla itself covers a relatively great distance as it wraps itself around the dorso-lateral surface of the prey; however in reference to the postfrontal and prefrontal bones, to which it is closely attached, the distance is slight.

Medial rotation of the palatine bone also aids in medially rotating the maxilla. When the mouth is open the maxillary process of the palatine

bone is directed dorso-laterad and the palatine process of the maxilla ventro-mediad. When the mouth is closed the maxillary process rotates ventro-mediad and (via the palato-maxillary ligament) rotates the palatine process dorso-mediad, thus restoring both of the processes to the same (approximately horizontal) plane. The slight adduction of the palatine bone in this region takes up the slack in the palato-maxillary ligament that would otherwise result from such movements. Descriptions of these actions are complicated by the fact that the terms " dorsal, ventral, lateral and medial" imply 90° relationships, whereas the bones themselves only rotate through 60-70 degrees at the most.

As has been noted in Part Two, the actions of the premaxillo- and the septomaxillo-maxillary ligaments are problematical as regards elevation and depression of the maxilla. Depression of the nasal component, it may be assumed, is of relatively little help in depressing the anterior end of the maxilla with reference to the prey.

D. Actions of the Mandible (Figs. 28-29, 33-34). The actions of the squamosal, quadrate, and mandibular bones during closing of the mouth produce extensive movements of the dentary bone; elevation, medial rotation, adduction, and retraction are involved. The axes of rotation, of course, are the same as those previously described in Part Two.

As shown by analysis of the cinefluorographs, elevation of the mandible occurs simultaneously around all three transverse axes of rotation in the mandibular complex: quadrato-mandibular, quadrato-squamosal, and squamosal-parietal axes.

All nine divisions of the adductor mandibulae musculature are effec-

tive in elevating the mandible around the transverse axis of the quadrato-mandibular articulation, though with varying degrees of efficiency. Those divisions with attachments on the cranium and palato-maxillary arch rotate the mandible around the squamosal-parietal articulation as well; these muscles include the adductores internus and profundus and the anterior and medial parts of the externus. The M. cervico-mandibularis also elevates the mandible around the squamosal-parietal articulation to some extent via the dorsad thrusting effect it has on the quadrate bone; however the main function of this muscle seems to be retraction of the mandible (vd. infra).

When the mouth is widely distended the anterior and medial divisions of the adductor externus and the adductor profundus are the most effective mandibular elevator, since they are directed dorso-rostrad from the compound bone. As the jaws are approximated, however, the adductors nearer the articulation (viz. adductor externus, pars posterior, and both parts of the adductor medius) are in more effective position to exert a dorsally-directed force. These last-named muscles connect the quadrate and mandibular bones. When the gape is wide the fibers are almost parallel to the two bones which form an angle approaching 180°; hence their effectiveness is reduced. As the more rostrally lying adductors contract, this angle is progressively decreased, thus permitting contraction of the posterior muscles to become more effective as they pull the quadrate and mandibular bones together around their common transverse axis.

The anterior division of the adductor internus muscle is of special interest in view of the fact that both origin and insertion are on highly

movable bones, viz. the mandible and ectopterygoid. In akinetic skulls, such as Alligator, the palatal region is firmly connected with the cranium, thus affording a stable muscle origin. In these akinetic skulls the insertion is on the mandible, and contraction of the muscle fibers gives a dorso-rostrad (protracting-elevating) pull. If, as in Alligator, the skull is monimostylic as well as akinetic, the only possibility of mandibular movement in this case is elevation; indeed, in the alligators this muscle is developed to a much greater degree than are the temporal adductors.

In snakes, however, with a kinetic skull structure, the palatal attachment of the anterior division of the internal adductor is on a highly movable bone. Hence contraction of this muscle not only elevates the mandible but even more importantly draws the ectopterygo-maxillary region ventrad and slightly mediad with reference to the prey. Furthermore, contraction of the muscle rotates the distal end of the ectopterygoid bone (to which it is attached) and the pterygoid teeth mediad around the longitudinal axis of the os pterygoideum. Thus in both skull types the contraction of this muscle elevates the mandible and depresses the cranium with reference to the prey; in the snakes the latter action occurs via the distal end of the maxilla and the postfronto-maxillary ligament. But in the ophidian skull the arrangement of the ligaments and rotational axes gives it the added function of medial rotator of the pterygo-maxillary arch. The muscle does not rotate the mandible because of its attachment into the medial, ventral, and lateral surfaces of the compound bone.

The posterior part of the internal adductor also serves as a medial rotator of the os pterygoideum when the mouth is distended, as has been shown.

Since it attaches ventro-medial to the mandibular longitudinal axis, and pulls dorso-medial when stretched over the surface of the prey, it could theoretically rotate the mandible laterally; however the much stronger elevators and medial rotators (vd. infra) would easily offset this action. Lateral rotation of the mandible occurs during opening of the mouth, as has been described. That the posterior part of the internal adductor does not operate during opening of the mouth may be reasoned from the fact that if it did it would rotate the pterygoid teeth medial, which direct observation shows does not occur. Hence the muscle aids in rotating the pterygoid teeth during closing of the mouth, and thus the lateral rotating effect on the mandible must be offset at this time by other muscles.

In snakes the posterior part of the internal adductor also seems to have some adducting action on the quadrato-mandibular region. The muscle pulls dorso-medially when the mouth is opened, but the passive resistance of the soft anatomy of the intermandibular region between the mandible and ventral midline prevents a dorso-medial force from adducting the mandible in this direction. Rather, the resultant of the ventro-medial force (resisting intermandibular anatomy) and the dorso-medial force (contracting adductor internus, pars posterior) moves the mandible directly medial. The other elevators of the mandible probably aid in this type of indirect adduction, but their cranial attachments lie more dorsad than does the pterygoid insertion of the adductor internus, pars posterior; hence these muscles are less effective in adducting the mandible.

The medial rotation noted by direct observation can only be explained by analysis of the direction of pull of the mandibular elevators; no other mus-

cles are in the proper position to produce this action. The insertion of the adductor externus, pars posterior and pars anterior, and the superficial part of the median adductor, all lie dorso-lateral to the longitudinal axis of rotation. Furthermore the fibers of these muscles all pass dorsal to the axis and insert on the quadrate bone and cranium at points medial to it. This is due, in the case of the quadrate attachments, to the torsion in the quadrate shaft which results in an antero-medial (instead of merely an anterior) insertion area for the mandibular elevators. Hence the quadrate attachments come to lie medial to the longitudinal axis of the mandible, and the musculature serves as a medial rotator as well as an elevator. The anterior part of the external adductor is probably the most effective medial rotator; it attaches on the lateral surface of the mandible and originates in the postfronto-parietal area far medial to the mandibular longitudinal axis.

Both the anterior adductor and the superficial part of the median adductor make up the bulk of the temporalis musculature. The adductor profundus and the medial portion of the adductor medius insert medial to the longitudinal axis of the mandible; hence it might be thought that they are in position to produce lateral rotation of the mandible as well as elevation. However the fibers of the former muscle are exceptionally weak, and those of the latter pull almost parallel to the shaft of the mandible in the vertical plane, i.e., almost directly dorsad; hence any lateral rotating effects they could possibly have are easily offset by the medial rotators which are much stronger.

Finally, the mandible is retracted strongly during closing of the mouth, as is shown by cinefluorograph and electrical stimulation studies. This

action is brought about by contraction of the cervico-mandibular muscle which passes dorso-caudally from its insertion on the distal end of the quadrate bone. The action of this muscle draws the quadrato-mandibular region dorso-caudad, the quadrate bone rotating around the transverse axis of the quadrato-squamosal articulation and the entire mandibular-squamosal-quadrate complex around the transverse axis of the squamosal-parietal articulation. Retraction of the os pterygoideum (contraction of the M. retractor ossis pterygoidei) may also assist in this movement, as the pterygoid bone pulls the mandible caudad via the pterygo-mandibular ligament. The resultant of these retracting forces and the elevating forces previously described tends to approximate the cranium and mandible, and at the same time thrusts the quadrato-squamosal region sharply dorsad; both of these effects are noticable in the living snake when the mouth is closed.

Thus the three chief ends outlined previously are attained. The dentiferous bones are drawn closer to the surface of the prey, thus bringing the teeth in position for a renewed grip. The dentiferous bones are also brought closer to each other, thus decreasing the size of the mouth opening and compressing the prey between the jaws. And finally, the dentiferous bones are drawn caudad, thus re-engaging the teeth in order to hold the prey while the contralateral side of the head is carried forward over the surface of the prey. When all of this has been completed the snake is again in position to begin the first phase of the deglutitional cycle anew.

Part Four: Further Considerations

The function of some of the other muscles of the cranial region of Elaphe, not previously mentioned, may be noted here. The following conclusions are inferred for the most part, since no direct proof of the muscle actions is at present available.

The MM. hyoglossus and genioglossus evidently are not used during deglutition; numerous observations made by the present investigator show that the tongue is never protracted during the actual swallowing process. At irregular intervals during deglutition the trachea is protracted, evidently by the M. geniotrachealis. During these intervals the mandible on one side is depressed somewhat and the trachea protracted rostro-laterad; at this time all ingesting activities cease and the snake takes several deep breaths before resuming swallowing of the prey. It may be assumed that the trachea is retracted by the M. hyotrachealis, but there is no direct evidence for this, and reinitiation of the swallowing activities is adequate to restore the laryngeal region to its normal position.

The glandular slips of the MM. transversus branchialis and intermandibularis anterior may serve as compressors of the sublingual gland. However the bulk of the prey would compress these glands in any case, so the statement is merely theoretical. It is likely that the buccal insertion of the M. transversus branchialis is used to pull the loose mucosa ventro-mediad around the sides of the trachea and tongue during opening of the mouth, thus preventing it from adhering to the prey when the mandible is subsequently protracted.

The costocutaneous muscles have been shown by Mosauer ('32) to play an important role in ophidian locomotion; their significance in deglutition, if any, is uncertain.

The MM. obliquus abdominis internus and transversus abdominis probably aid the esophageal musculature in forcing the prey toward the stomach once it has passed the jaw region. However there is no direct evidence for this statement. The two muscles surround the esophagus entirely, and hence are in position to act as esophageal constrictors. In the absence of any direct evidence it may be assumed that the M. constrictor colli also aids the esophageal musculature after the prey has passed the cranial region. Like the two muscles surrounding the esophagus, the constrictor colli encircles almost the entire neck region. Direct observation shows that during the swallowing process the neck region is definitely constricted immediately rostral to the prey, but whether this is due to any, all, or none of these muscles has not as yet been shown.

Part Five: Discussion

In his extensive analysis of the egg-eating adaptations in Dasypeltis Gans ('52) remarks that the ingestion method used by most snakes has been so often described in the literature as almost to obviate restatement. However he gives no references, nor has the present writer been able to locate any analysis of the method that could rightly be called comprehensive. There are many statements in the literature concerning various phases of the jaw action, but there is at the same time much disagreement among workers regarding the

causal elements involved in moving the various bones of the head. Haas ('31b), Versluys ('37), Cowan & Hick ('51), and Gans ('52) discuss some phases of the deglutitional cycle in detail, and Cowan & Hick even attempt a comprehensive outline of the action sequences. But until now there has been no investigation of the cranial articulations and ligaments, and hence all previous investigations have been inadequate at least to some extent. Thus it is not surprising that much disagreement exists among workers regarding numerous phases of the general problem of ophidian deglutition.

For instance, Gans ('52) and other workers have noted that in snakes a two-phase cycle exists. Cowan & Hick ('51) recognized this possibility, but "in the absence of evidence" (p. 53) they assume that a four-phase cycle occurs; that is, each maxilla and each mandible moves independently. This erroneous assumption is the primary reason why much of the functional material presented by these workers is incorrect, though other factors also are involved.

Thus Cowan & Hick do not recognize mesokinetism in snakes (which has long been known), and hence picture (Figs. 1, 2) a firm connection between the dorsal laminae of the frontal and nasal complexes; however, as has been shown, the fronto-nasal articulation is definitely movable, and of great importance in controlling the movements of the palatine bone and the rest of the palato-maxillary component. As has been indicated, the vomer and premaxilla do not form a functionally independent unit leaving the remainder of the nasal component firmly fused to the rest of the cranium (as they suggest); on the contrary, the entire nasal component is firmly bound together and functions as a controlling mechanism in adjusting the dentiferous bones of the palato-

maxillary arch to various phases of the swallowing process. Cowan & Hick likewise consider the pterygo-palatine articulation to be firm, and hence assign no movements around the two axes of this saddle articulation. Thus it is not difficult to appreciate why their analysis of the movements of the upper jaw is, unfortunately, simple but incorrect.

The longitudinal axes of rotation have generally been overlooked in discussions of the ophidian cranial kinetics; the importance of these axes has been continually emphasized in the previous pages. Thus, investigations prior to this have recognized only a simple hinge joint at the quadrato-mandibular articulation, instead of the saddle type which allows longitudinal mandibular rotation as well as elevation-depression. Hence the rotating functions of the temporal adductors and the intermandibular muscles are not taken into consideration, and the complicated development of these groups of muscles not properly analyzed. Cowan & Hick seem to be the first to have recognized a division of the median adductor of the mandible into superficial and deep portions, but they do not correlate this with the longitudinal rotation of the mandible, as has been done here. They recognize the fact that the internal adductor, pars anterior, is attached to movable bones at both ends, but because they postulate a four-phase deglutitional cycle their analysis of the functions of this muscle is of necessity inadequate; it would seem that their own interpretations of the functions of the muscle are not borne out by other data presented elsewhere in their paper. It may also be noted that the longitudinal rotating effects on the pterygoid bone following contraction of the posterior part of the internal adductor are not taken into consideration by

these workers, and hence they assign this muscle to the opening phase of the deglutitional cycle, rather than to the closing phase.

The present writer also questions the statement of Cowan & Hick that the mucosal division of the transverse branchial muscle is used to evenly distribute the mucosa over the greatly distended surface of the oral cavity when the mandibles are abducted. The muscle attaches into much too small an area of the mucosa to achieve this end, not to mention the fact that contraction of a muscle would not spread out the soft anatomy to which it is attached.

Haas ('31b) and Gans ('52) both remark on the unusually strong development of the M. cervico-quadratus in Dasypeltis, but in company with other workers they have not assigned a function to this muscle. As Gans notes, however, the squamosal-parietal articulation in Dasypeltis is well developed. Thus the function attributed to it by the present writer would seem to be confirmed; extensive depression of the squamosal-quadrate-mandibular complex is essential in an egg-eating snake, and the muscle is in the proper position to achieve this end.

Cowan & Hick speculate at length on the lingual retracting effects of contraction of the hyoglossus musculature. The main problem seems to lie with the fact that, according to them, the posterior ends of the ceratohyals (from which these muscles originate) are not attached to the gastrosteges and hence not firmly stabilised. Gnanamuthu ('37) has suggested that the lingual retraction mechanism is in effect due to the elastic recoil of the ceratohyals themselves which during tongue protraction have become flexed by the contraction of the genioglossus musculature. As has been shown, however, the hyoid

head of the neuro-costo-mandibularis muscle actually does insert into the midline of the gastrosteges, and thus fixes the ceratohyals firmly when the genioglossi contract.

It may also be noted here that Edgeworth ('35) assigns the neuro-costo-mandibular muscle to the hyoid group on the basis of embryological evidence. However, as has been remarked, Edgeworth's views have been sharply challenged in the literature, and the present writer has not been able to confirm the hyoid origin of this muscle from electrical stimulation of the facial nerve.

As regards the intramandibular articulation, J. T. Gregory ('51) states that a splenio-angular articulation is found only in the mosasaurs and in Hesperornis, a toothed bird of the Cretaceous. As will be shown in Section Two, this statement is not borne out by subsequent investigations, and the significance of the articulation in snakes ought not be underestimated. McDowell & Bogert ('54) have emphasized the importance of this joint in the platynotan lizards and in the snakes, vd. infra.

In general, the remarks of the previous paragraphs are made only to give some indication of the disagreement among workers regarding the functional aspects of various features of the ophidian jaw mechanism. There is in effect an insufficient amount of work on the functional aspects of deglutition to justify a detailed critique of the work of the few investigators who have entered this field; most of them were laboring with limited data. Cowan & Hick have discussed the general problem in some detail, but in view of their basic assumption that the ophidian swallowing cycle is four-phase, it is little wonder that their work and the present investigation fail to support each other.

Section Two

The Phylogenetic Development of Ophidian Cranial Kinesis

An analysis of the foregoing chapters provides at least a partial understanding of the kinesis of ophidian jaws, and an appreciation of the complexity of the cranial interrelationships that have evolved in snakes. No other sauropsid, or vertebrate for that matter, shows the high degree of kinetism and streptostylism found in the ophidian suborder. The nearest ophidian relatives, the lizards, make an approach though even in these forms the jaw structure is designed along more simple lines.

Detailed comparisons between lizards and snake cranial kinesis is precluded by the lack of information on the functional aspects of the saurian swallowing mechanism. Nevertheless, a morphological investigation of the skull of several carefully selected saurians allows one to make some instructive comparisons. There is sufficient material to allow us to trace at least the main trends in the evolutionary development of the swallowing mechanisms, and to show how the basic morphology of the ophidian jaw apparatus is developed from the preadaptive characters found in the lizards. Since the structures of the cranial region, and especially the morphology of the skull, play such an important part in the classification of reptiles, it is fortunate for our purposes that the cranial osteology of the lizards has been worked out in some detail, though there are notable gaps in the fossil record.

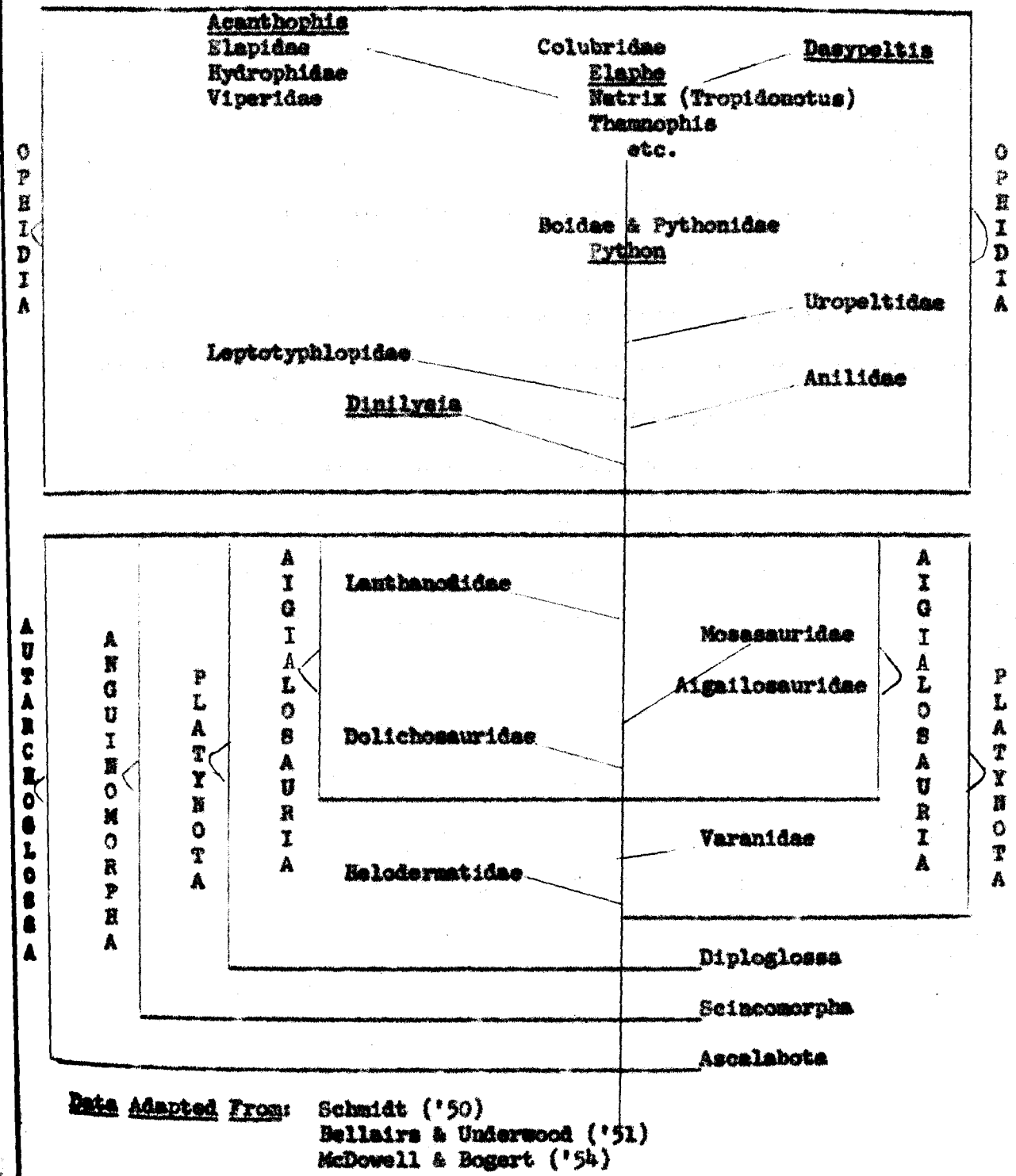
Within recent years a new interest has arisen in the origin of the snakes, as is evidenced by the extensive monograph of McDowell & Bogert ('54)

and the review article of Bellairs & Underwood ('51). Both of these publications re-emphasise the view long held that the snakes are derived from the Autarchoglossan lizards, infraorder Anguinomorpha, superfamily Platynota. It is the purpose of the remainder of this chapter to analyse the morphology of the platynotans and the ophidians from the standpoint of cranial kinesis, and thereby outline the functional trends in the jaw development which culminate in the generalised advanced snakes, of which Elaphe is an example. No attempt is made here to strengthen or oppose current views on reptilian phylogeny; much more than mere jaw structure must be analyzed if any systemic revisions are to be attempted. The present writer is here concerned with trends in the development of the ophidian deglutitional apparatus, rather than with the phylogeny of this particular group of reptiles. The most up-to-date and authoritative classifications of the Platynota and Ophidia are here assumed to be correct; the references to systematics in the following pages are based on this premise.

Part One: Classification of the Anguinomorphan Lizards and the Snakes

The lizards have been classified into two main groups by Camp ('23): the Ascalabota and the Autarchoglossa. The Ascalabota include such forms as agamids, iguanids, and chameleons; these on the whole are more primitive than the Autarchoglossa. The latter are divided into two main groups, the Scincomorpha and the Anguinomorpha, characterised chiefly by the reduction or loss of limbs. The Scincomorpha, as the name implies, includes the skinks, as well as some other less-familiar forms. The Anguinomorpha, with which we are here

Interrelationships of the Lizards and Snakes Discussed in Section Two



Data Adapted From: Schmidt ('50)
Bellairs & Underwood ('51)
McDowell & Bogert ('54)

concerned, are characterized by a unique tongue, alternate and inter-dental tooth replacement, and several distinctive skeletal features. These last include: unpaired premaxilla without a median tooth and pierced by a foramen, a distinct angular bone, and the Meckelian groove open anterior to the splenial bone.

The Anguinomorphs have been divided by McDowell & Bogert ('54) into two superfamilies, the Diploglossa (or Anguinoidea) and the Platynota (or Varanoidea). The Diploglossan lizards include many fossil forms, as well as the extant California limbless lizard, Anniella, and others. This group retains the more usual (and seemingly more primitive) saurian jaw apparatus, modified chiefly for the crushing and chewing habits characteristic of these insectivorous lizards. The bones of the lower jaw are all firmly fused together, and in many instances the sutures are obliterated. The single dental row of the dentary bone (and of the maxilla) is continued back beneath the orbit, the posterior teeth thus being nearer the elevating musculature of the mandible and in a more mechanically efficient position for effective crushing. In the upper facial region added strength is afforded by the bones of the maxilla which are arranged to form a curved transverse buttress anterior to the orbit. Numerous other features of the Diploglossan jaw structure are characteristic, but they need not concern us further here.

The second division of the Anguinomorpha, the Platynota, are characterized by a jaw structure adapted for the capture, rather than the mastication of food. The jaws are used for grasping rather than for crushing; hence the mandible and maxilla show evidence of anterior displacement of the tooth row,

which comes to lie entirely anterior to the orbit. This change reduces the crushing power, which is of less importance in the capture of squirming prey, but increases the speed with which the rostral end of the jaws may be snapped together. The characteristic sharply recurved teeth also aid in preventing the escape of the prey.

The forward displacement of the tooth row results in the lengthening of the snout as well. However the buttressing effect of the bones of the facial region is based on a different principle from that found in the Diploglossa. As McDowell & Bogert ('54) have shown (p. 107), in the Platynota the principle of polylamination is employed. The external narial fissure is extended back as far as the frontal bone (as in Elaphe), thus separating the facial region into paired lateral prefronto-maxillary struts and a rostromedian nasal strut. The arrangement affords sufficient strength to the nasal region without adding the excess weight that hypertrophy of the bones would entail, if they were arranged in the transverse (Diploglossan) manner.

The platynotan lizards have been most recently classified into six families by McDowell & Bogert ('54). These include the Helodermatidae, represented by the Gila Monster (Heloderma) of the southwestern United States, and the Varanidae, represented by numerous forms of the genus Varanus. Four Families (Aigialosauridae, Mosasauridae, Dolichosauridae, and Lanthanotidae) compose the "Aigialosaurian Group"; the first three are extinct. The last Family consists of a rare monotypic genus, Lanthanotus, which shows many advanced characteristics that place it on a more direct line to the ophidians than are any of the other known Platynota.

Without going into numerous details, we may outline the interrelationships of the above six groups, as modified by McDowell & Bogert ('54) from Romer ('45) and Camp ('23). The Helodermatidae show features, such as a poorly-developed intramandibular hinge and an anguinid-like brain case, that set them off as the most primitive of the living Platynota. The Varanidae show more advanced modifications in the form of the skull and arrangement of the soft anatomy. The Dolichosauridae, Algaiosauridae, Mosasauridae, and Lanthanotidae all show characteristics that unite them in a rather closely-knit group; these features include a reduction in phlangeal count and a more highly-developed intramandibular hinge. It must be emphasized that the known platynotan forms, both fossil and extant, do not show a smooth progressive ascent from primitive to recent; all have at least some specialized features which indicate that radial adaptation from a generalized platynotan stock has occurred at all levels.

Like the Platynota, the Ophidia also show a great deal of adaptive radiation, although there is a general agreement regarding the members of the primitive and recent groups. The Pythonidae are recognized as a generalized primitive group, though more advanced than some fossil forms and the extant but specialized Anilidae, Leptotyphlopidae, and Uropeltidae. The Colubridae compose a vast assemblage of basically generalized forms (as compared with the Viperidae, Elapidae, Hydrophidae, etc. derived from them), but even these have radiated to almost every habitat, as has been pointed out by Schmidt ('50). [illegible] represents a generalized epigean colubrid, and is used here as a type [illegible]ple.

In the following pages five representatives of the platynotan-ophidian line have been selected to illustrate the progressive development of the jaw region leading to the highly kinetic swallowing apparatus found in the generalized colubrids. These forms are Heloderma (a primitive platynotan), Varanus (a more advanced platynotan), Lanthanotus (a representative aigialosaurian lizard, leading to the ophidian line), Python (a primitive generalized snake), and Elaphe (a recent generalized snake).

As has been mentioned, the line is not a straight one. Hence upon the generalized pattern of each form are at least some superimposed specializations. It should again be noted that only certain features of the deglutitional mechanism are mentioned in the following pages, and numerous features of significance in phylogeny are not discussed at all.

The present investigator has relied on McDowell & Bogert ('54) for information on Lanthanotus. The anatomy of this rare lizard (of which there is only one specimen in the Western Hemisphere) has not yet been worked out completely, and there is as yet no published data on the musculature.

Part Two: Platynotan-Ophidian Kinesis

The Nasal Region
(Table I)

The general trend in the phylogenetic development of the nasal region is characterized by a progressive freeing of the bony attachments of the maxilla, the incorporation of the vomer into the nasal component from its primitive position at the rostral end of the palatal arch, and the change in function of the prefrontal bone from a supporting strut to a moving fulcrum.

Table I

Phylogenetic Trends in the Development of Colubrid Cranial Kinesis

Part One: Nasal Region

	Heloderma	Varanus	Lanthanotus	Python	Elaphe
A. Maxilla					
1. Osseous connections					
Premaxilla	x	x	x	o	o
Vomer	x(*)	x	o	o	o
Septomaxilla	x	x	x	o	o
Prefrontal bone	x	x	x	o	o
Palatine bone (direct or indirect)	x	x	x	o	o
Complete postorbital arch	x	o	x	o	o
Ectopterygoid bone	x	x	x	x	x
2. Relative extent of facial process	xxx	xxx	xx	x	o
B. Vomer					
Osseous connections					
Premaxilla	x	x	x	x	x
Maxilla	x(*)	x	o	o	o
Fused median septum	o	o	x	x	x
Palatine bone	x	x	x	o	o
Frontal bone	o	o	x	x	x
C. Prefrontal Bone					
Osseous connections					
Maxilla	x	x	x	o	o
Descending lamina of frontal bone	x	x	x	o	o
Palatine bone	x	x	x	o	o

(*) In some species

The progressive reduction of the osseous attachments to the maxilla is the most apparent of these features. In the Platynota this bone is firmly bound to the other bones of the nasal and orbital regions. In the snakes (at least in those lacking specializations for burrowing) the maxilla is closely attached only to the ectopterygoid bone, and even in these forms there is a high degree of movement possible at this articulation. The most important advantage of this reduction of osseous attachments is freedom for longitudinal rotation which is thereby gained, and made possible also by the presence of ligaments and by the reduction of the facial process of the maxilla itself. In some specialized colubrids certain of these osseous connections have been re-established, as is the case of the premaxillo-maxillary articulation in Dasypeltis; this last is a secondary modification in keeping with the egg-eating specializations of this genus (Gans, '52). The incomplete postorbital arch of Varanus is also considered a specialization (McDowell & Bogert, '54).

The vomer undergoes extensive modification during the phylogenetic development, changing its position and attachments from the palato-maxillary arch to the nasal complex. Though primitively joined to the maxilla and palatine bone, as well as the premaxilla, it gradually fuses into the mid-septal region to form part of the ventral surface of the nasal component of the skull. However it retains its ligamentous connections with the palatine bone (palato-vomerine ligament) even in the advanced colubrids, though the palatine bones become progressively more movable as the kinesis of the palato-maxillary arch is increased. The joining of the vomer with the descending lamina of the frontal bone is found in both Lanthanotus and snakes, and results from the concom-

itant progressive descent of the frontal descending laminae (vd. infra) and the dorsal lifting of the vomer from the palato-maxillary arch to the nasal component.

An important change takes place in the functioning of the prefrontal bone (together with the lacrimal bone in lizards). As the maxilla loses its firm osseous connections, the prefrontal bone in turn loses its function as a supporting strut in the preorbital region. Therefore its connection with the descending lamina of the frontal bone is decreased in extent, although the lamina itself progressively increases in size. The prefrontal bone is orientated chiefly in the transverse plane, at right angles to the descending vertical lamina of the frontal bone. Fusion of these bones along their common vertical axis would result in locking of the prefrontal bone to the frontal, and prevent its abduction-elevation along a longitudinal axis. This in turn would limit abduction-elevation of the maxilla, which remains attached to the prefrontal bone by a strong prefronto-maxillary ligament. Hence in the advanced snakes the prefrontal bone is attached only to the dorsal surface of the frontal bone. Thus in Elaphe the prefronto-frontal articulation is movable, as described previously.

The results of these changes may be summarized as follows. In the primitive Platynota (Heloderma) all the bones of the upper jaw from the postorbital region rostrad are firmly fused and function as a unit. Progressive loosening of the osseous connections results in the condition found in Elaphe. The platynotan preorbital supporting strut (maxilla, prefrontal, and frontal bones) becomes movable and loses its primitive function. The maxilla is freed

almost entirely, allowing the longitudinal rotation, abduction, and elevation which have become so important in the colubrid mode of feeding. The edentulous vomer loses its close union with the dentiferous bones of the palato-maxillary complex and becomes incorporated into the nasal component; this last in turn is further strengthened by the fusion of the nasal bones, vomers, and septomaxillae into a median vertical septum, thus providing a means for efficiently dissipating the upward thrust of the prey caudad to the brain case. The palatine bone, together with the posterior extension of the palato-maxillary arch, is thus freed from firm connections with the maxilla and nasal component, and in Elaphe can move around all three chief axes, rather than in a rostro-caudal direction only. Hence in advanced colubrids the dentiferous bones of the upper jaw are able to move in the complicated manner outlined previously.

Part Three: Platynotan-Ophidian Kinesis

The Brain Case Region
(Table II)

The numerous phylogenetic modifications that occur in the brain case region are of great significance in the development of the ophidian swallowing mechanism. Chief among these is the development of vertical laminae from the horizontal lamina of the combined frontal and parietal bones. These vertical osseous extensions not only wall of the brain case laterally and ventrally, but change the cranial kinesis from the saurian metakinetic to the ophidian mesokinetic type. In addition, they present added room for attachment of the constrictor dorsalis musculature which reaches its most advanced development in the snakes.

Table II

Phylogenetic Trends in the Development of Colubrid Cranial Kinesis

Part Two: Brain Case Region

	Heloderma	Varanus	Lanthanotus	Python	Elaphe
A. Frontal Bone					
Osseous connections					
1. Horizontal lamina					
Parietal bone	x	x	x	x	x
Nasal bone	x	x	x	o	o
2. Descending lamina					
Parietal bone	o	o	o	x	x
Nasal bone	x	x	x	x	x
Vomer	o	o	x	x	x
Palatine bone	x	o	x	o	o
Prefrontal bone	x	x	x	x	o
Basisphenoid bone	o	o	o	x	x
Contralateral lamina	x	x	o	o	o
B. Epipterygoid and Parietal Bones					
1. Epipterygoid bone	x	x	x	o	o
2. Parietal bone					
Osseous connections					
(a) Horizontal lamina					
Frontal bone	x	x	x	x	x
Supraoccipital bone					
ventral surface	x	o	o	o	o
posterior surface	o	x	x	x	x
(b) Descending lamina					
Frontal bone	o	o	o	x	x
Prootic bone					
rostro-dorsal edge	x	x	x	x	x
dorsal edge	o	x	x	x	x
anterior edge	o	o	o	x	x
Basisphenoid bone	o	o	o	x	x

In Heloderma and Varanus the frontal and parietal bones articulate only along a transverse line on the dorsal surface of the skull. This could theoretically allow the frontal and parietal bones to rotate around their common transverse axis, were it not for the postorbital and temporal arches. However, with the progressive development of the descending processes of the frontal and parietal bones, this potential articulation becomes an impossibility.

At the anterior end of the frontal complex in the Platynota, the horizontal lamina is fused transversely with the horizontal (dorsal) lamina of the nasal bones. With the progressive descent of the vertical frontal laminae and consequent fusion with the vertical (median) septum of the nasal complex, this fronto-nasal articulation also becomes locked. In the snakes the horizontal lamina of the fronto-nasal complex becomes separated and the two are joined only by the fronto-nasal ligament. Thus the nasal component is free to rotate on the descending laminae of the frontal bones, thus in turn giving rise to the mesokinetic type of skull which is characteristic of snakes. The other modifications of the brain case region are consequent to this basic change in kinesis.

The concomitant fusion of the vomer with the nasal component and the progressive descent of the vertical laminae of the frontal complex results in the articulation of the two. In Lanthanotus, in which the palato-maxillary arch is still relatively fixed to the rest of the skull, the frontal descending processes even fuse slightly with the dorsal surface of the palatine bones; in the more primitive Varanus the frontal bones have not descended sufficiently far to effect this union.

The rostral development of the basisphenoid bone also progresses phylogenetically until in the snakes the bone finally fuses with the descending processes of the frontal complex and thus walls off the anterior brain region (olfactory tracts) ventrally. In the Platynota this fusion has not as yet taken place; in Heloderma and Varanus the paired frontal descending processes actually fuse with each other ventrally, but in Lanthanotus they remain separated and thus presage the consequent independent fusion to either side of the anterior basisphenoid bone.

In the saurian metakinetic skull the main transverse articulation occurs at the parietal-supraoccipital junction. However in the primitive Heloderma the rostral edge of the supraoccipital bone is connected with the ventro-posterior surface of the os parietale. In Varanus and more advanced lizards this articulation shifts caudad to a dorsal edge-to-edge union of the two bones. With the development of the parietal descending laminae and fusion of the prootic bone with the parietal and supraoccipital bones, this functional articulation is lost. Thus the brain case region becomes progressively modified from the kinetic type found in the Platynota (metakinetic skull) to the functionally single, closely-knit unit characteristic of the cranial component of snakes (mesokinetic skull).

In Varanus a transverse axis of rotation occurs at the fronto-parietal articulation, but this is only made possible by the lack of a complete postorbital arch in these forms, which is a secondary modification of Varanus as has been mentioned.

Together with these developmental changes is the lack of the epipterygoid bones in snakes, and the firm fusion of the basisphenoid bone with

the ossa frontalia, parietale, and prootica on the ventro-lateral surface of the brain case.

Part Four: Platynotan-Ophidian Kinesis

The Pterygoid Bone and the Mandibular Region (Table III)

The pterygoid bone in all the forms under discussion is bound posteriorly to the quadrate region by the pterygo-mandibular ligament. Anteriorly, however, progressive modification occurs, in keeping with the changes in the general kinesis of platynotan and ophidian skulls. In the lizards the pterygoid bone is firmly articulated with the palatine and ectopterygoid bones, thus transmitting forces directly rostrad to the upper jaw region. In the snakes, however, the pterygo-palatine articulation becomes progressively less firm, until in the advanced colubrids there is found a saddle joint of the type described in Elaphe. Thus the pterygoid bone becomes relatively independent of the various actions of the bones in the anterior region of the skull. The pterygo-ectopterygoid articulation becomes more freely movable as well, and hence the rostrad force-transmitting function of the pterygoid bone is still effective, although the variations in the relative position of the maxillary and palatine teeth are numerous. Furthermore, this general freedom of the pterygoid bone (together with the loss of the epipterygoid bone in snakes) allows it to rotate around the longitudinal axis as well.

In the Platynota the mid-dorsal surface of the pterygoid bone articulates with the basisphenoid in a sliding joint, anterior to which the os pterygoideum is horizontally flattened to provide insertion area for the leva-

tor and protractor ossis pterygoidei musculature. In Python the basisphenoid articulation is lost altogether. In this last form the pterygoid vane is flattened posteriorly more than anteriorly, thus allowing additional area for the insertion of the constrictor dorsalis musculature, the development of which progresses rapidly in the Ophidia in keeping with the added functional importance of the pterygoid bone. It may be noted that the absence of a pterygo-basisphenoid articulation in higher snakes permits abduction of the pterygoid bone and palato-maxillary arch; and the quadrato-mandibular region also is thus free to move medial and lateral as well.

Table III

Phylogenetic Trends in the Development of

Colubrid Cranial Kinesis

Part Three: Pterygoid and Lower Jaw

	Boioderes	Yarrmus	Lanthanotus	Python	Elaphe
A. Pterygoid Bone					
Palatine connection firm	x	x	x	o	o
Basipterygoid process	x	x	x	x	o
Anterior horizontal flattening	x	x	x	x	o
Posterior horizontal flattening	o	o	x	o	x
B. Mandible					
Quadrate suspension:					
via paroccipital process	x	x	x	o	o
via squamosal	x	x	x	x	x
Fused mental symphasis	x	x	x	o	o
Lateral vertical hinge	o	x	x	x(*)	x(*)
Medial vertical hinge	o	o	x	x	x
Height of splenial bone as compared with mandible	-1/2	-1/2	-1/2	-1/2	-1/2

*) Lateral surangular process secondarily developed

Of all the cranial modifications in the platynotan-ophidian line, those pertaining to the lower jaw are most striking. In the lizards the quadrate bone, though movable, is attached to the paroccipital process of the exoccipital bone, to the squamosal (tabular of some authors), and to the posterior end of the superior temporal arch if the latter is present (e.g. Varanus). In Lanthanotus and the primitive fossil snake Dinilysia the quadrate is supported by both the paroccipital process and squamosal bone (McDowell & Bogert, '54). However in generalized recent snakes the suspension is limited to the squamosal bone alone, thus allowing the quadrate bone and mandible to move in a rostro-caudal direction. Longitudinal prolongation of the squamosal bone, together with its movable articulation on the parietal bone, gives the lower jaw added area over which to move.

A second feature of importance is the degree of fusion at the mental symphasis. In the Platynota the anterior tips of the dentary bones are fused relatively firmly, though without a true synostosis. In the snakes the mandibles are entirely separate, thus allowing each jaw to work independently, as is characteristic of the ophidian deglutitional process.

In keeping with the phylogenetic development of modifications to accommodate large, active prey, is a progressive trend toward the formation of a functional intramandibular articulation. In Heloderma the bones of the mandible are firmly fused together, and allow no true interosseous flexion. The mandible of Varanus shows the dentary and surangular bones arranged in such a way that their common articulation forms an approximately vertical line on the lateral surface. In Lanthanotus the splenial and angular bones as well articulate along a vertical line on the medial surface of the mandible, almost dir-

ectly opposite the lateral dentary-surangular hinge line. Thus there is formed in the middle of the mandible a "zone of weakness" which preadapts the mandible for the development of a true functional hinge as found in the snakes.

This "varanid hinge", as it has been called, has been of interest for a long time. It is one of the characteristics of the Platynota as a group, and is correlated with increased size of the gape found in these forms. A convergent condition was long ago noted in the European Nightjar (Aves) by C. L. Nitzch (1811, 1815), and discussed more recently by Lubosch ('29). Perhaps this represents an adaptation of these birds towards increasing the gape, a decided advantage to forms such as these which capture their insect prey while in flight.

J. T. Gregory ('51, '52) has pointed out a similar convergent development of an intramandibular articulation in the extinct tooth bird Hesperornis, a fish-eater of the Cretaceous, and first described by Marsh in 1880. Gregory has also discussed in detail the anatomy of the intramandibular articulation in the mosasaurs (Aigialosaurian lizards, vd. supra), which was first described by Williston (1889). McDowell & Bogert ('54) state that the intramandibular articulation has reached its most perfect state in the mosasaurs, the specialized leptotyphlopid snakes excepted. From an overall functional standpoint, however, this statement may be questioned, since the streptostylism in snakes and the lack of intermandibular union has reached a far greater degree of development than in any known mosasaur. When the details of the intramandibular articulation as found in Elaphe are analysed (Chapter IV) and compared with Gregory's description of the mosasaurian condition, a great deal of

similarity is immediately apparent. The secondary development of the lateral process of the compound bone in snakes, however, masks the simplicity of the articulation, and may easily lead to erroneous conclusions regarding the functional efficiency of this joint.

Finally, it may be noted that there is a progressive decrease in size between the articulating surfaces of the main bones of the intramandibular hinge (viz. splenial and angular). In the snakes this results in a relatively smaller degree of osseous union between the anterior and posterior elements of the mandible, and makes for greater adaptibility of the dentary bone in conforming itself to the shape of the struggling prey, especially when the mandible is curved in the vertical plane around the (usually) cylindrical prey when the mouth is open.

Part Five: Platynotan-Ophidian Kinesis

The Dentition
(Table IV)

Not a great deal can be said regarding the dentition of the Platynotans and Ophidians, since great variation in number and size and shape of the teeth is of common occurrence, and mirrors the extensive radial adaptation the lacertilians have undergone as regards specific food habits. However some comparative generalizations may be profitable.

The teeth of both the platynotans and the snakes are modified for the handling of live, struggling prey; hence they are curved sharply caudad. The primitive Heloderma shows this to a slight extent. In Varanus and Lanthanotus the teeth are curved backward to a somewhat greater degree. In the snakes,

Python and Elaphe, they are pointed back to such an extent that the distal half of the tooth is almost parallel to the plane of the substrate. This condition in snakes not only aids in holding the struggling prey, but also assists the teeth in sliding rostrad during protraction of the dentiferous bones.

Table IV

Phylogenetic Trends in the Development of Colubrid Cranial Kinesis

Part Four: Dentition

	Boiga	Natrix	Lampropeltis	Python	Elaphe
Number of teeth (app.)					
Premaxilla	8	8	8	4	0
Maxilla	8	12	12	18	19
Palatine bone	2-3	0(*)	2-3	6	10
Pterygoid bone	4-5	0(*)	12	12	21
Dentary bone	9-10	12	12	17	21
Cross-section through crown					
Round	x	o	o	o	o
Longitudinally ellipsoidal	o	x	x	x	x
Degree of caudal curvature	x	xx	xx	xxx	xxx
Degree of medial curvature on posterior dentary bone	o(**)	x	x	xx	xxx

(*) Teeth on some fossil genera, e.g. Saniwa (McDowell & Bogert, '54)
(**) Highly variable

The teeth of both Python and Elaphe are curved sharply mediad as well as caudad along the posterior end of the dentary bone. In a form such as Elaphe in which the intramandibular articulation is well developed, adduction

and lateral rotation of the anterior end of the dentary bone will abduct the superior lateral process of the bone as well as rotate it laterally. In order for the posterior teeth to be effectively disengaged, at least some degree of medial as well as caudal curvature is necessary. The same tooth arrangement, of course, is advantageous during medial rotation of the mandible, which occurs when the lateral adductor mandibulae musculature contracts.

Correlated with this condition is the cross-sectional pattern of the tooth crown. In Heloderma, as well as the more primitive Diploglossans generally, the tooth crown is circular in cross-section; in Heloderma this is secondarily modified by venom grooves. A round cross-sectional pattern is an adaptation for receiving vertically directed forces. In the Diploglossa the jaw apparatus is used chiefly for a crushing bite; in Heloderma the vertically directed forces are applied in holding the prey while the venom takes effect, though the tooth pattern is also a hold-over from the anguinomorphan ancestors common to both the Diploglossa and Platynota.

In the advanced Platynota and the snakes, however, the main resisting forces are orientated longitudinally to the skull. Hence the tooth crown is ellipsoidal in cross-section, with the long axis parallel to the long axis of the skull. Thus the tooth is strengthened more for preventing the escape of the struggling prey than for crushing it between the jaws.

As regards the number of teeth on the dentiferous bones, only generalizations are possible, as has been mentioned, and even these are hazardous owing to the variations found from specimen to specimen. In general there is a phylogenetic increase in the number of teeth on each of the dentiferous bones,

except the premaxilla. In view of the increased movement of the palato-maxillary arch and the development of the fronto-nasal hinge which allows the nasal component to be elevated, the premaxillary teeth become of less importance functionally, and thus in the advanced colubrids such as Elaphe the premaxilla is edentulous.

Part Six: Platynotan-Ophidian Kinesis

Cranial Musculature

The comparative data on the cranial muscles of the five platynotan and ophidian forms under discussion is extremely limited. In Lanthanotus there is no data whatsoever. In Heloderma, Varanus, and Python there is some information available in the literature, especially as regards the dorsal constrictor musculature, but no sufficiently precise material is to be had on the intermandibular and posterior throat musculature. Hence any overall attempt to compare the musculature of the five forms is out of the question at present. The data that is available is summarized in the following pages as a preliminary step to future more comprehensive work.

The five constrictor dorsalis muscles of the snakes are represented by three muscles in the saurians: MM. protractor ossis pterygoidei, levator ossis pteyygoidei, and levator bulbi oculi; the last is divided into dorsal and ventral divisions. The highly kinetic palato-maxillary arbh of snakes necessitates extensive modification and division, since the palatine and pterygoid bones in these forms become relatively independent in action with the development of a saddle joint at their common articulation. In the Ophidia

the M. levator bulbi oculi becomes the MM. retractor ossis pterygoidei and retractor vomeris (Lakjer, '26). The attainment of a freely-movable nasal component readily explains the separation of the M. levator bulbi oculi into palatine (retractor ossis pterygoidei) and vomerine (retractor vomeris) slips in the Ophidia. The M. levator ossis pterygoidei is much more highly developed in snakes than in such forms as Varanus, in which abduction of the pterygoid bone is prevented by the pterygo-basisphenoid articulation. The splitting of the primitive M. protractor ossis pterygoidei into protractors of the pterygoid and quadrate bones seems to be a relatively late occurrence among the Ophidia, and in the absence of more extensive comparative data little can be said with certainty. Even in advanced colubrids (such as Tropidonotus) the M. protractor ossis quadrati sometimes has a quadrate rather than a mandibular attachment as in Elaphe and Thamnophis, indicative of the unstable condition of this muscle in snakes.

In the absence of any information on muscles in Lanthanotus little can be said about the phylogenetic development of the complex adductor mandibulae musculature. Lanthanotus represents an intermediate form between the "open" brain case found in Varanus and the "closed" condition characteristic of the Ophidia. We may hope that when information on the brain case insertions is had for Lanthanotus we may better be able to trace the development of the mandibular adductors.

It may be noted here that the M. adductor mandibulae internus is not divided into anterior and posterior divisions in Acanthophis (McKay, 1889), but extends to the mandible from a continuous attachment along the caudal edge of

the os ectopterygoideum and the ventro-lateral surface of the posterior half of the pterygoid bone. Since Acanthophis is a proteroglyph, and hence supposedly a highly-specialized derivative of the Colubridae, the question arises as to the status of this muscle. In Python (Scortecci, '39) as well as in Elaphe it is divided; hence we must again await more extensive comparative studies on the cranial musculature of the Ophidia before drawing any conclusions concerning this muscle.

As is apparent, any serious attempts at comparing the cranial muscles of the Platynota and Ophidia must await the completion of much more work on individual forms.

Part Seven: Platynotan vs. Ophidian Jaw Mechanisms

There exists no work on the functional anatomy of the deglutitional apparatus in any lacertilian (or other reptile, for that matter) that is comparable in scope to that attempted in the present investigation. And in the absence of sufficient data on the cranial musculature of the Platynota, extensive comparisons of the mode of feeding of snakes and their nearest saurian allies becomes speculative to a great extent. Some remarks of a general nature are possible however. Nevertheless they are admittedly based more on negative evidence than positive information and hence remain in the realm of speculation for the most part.

Among the Platynota, protraction of the pterygoid bones can have but one result: elevation of the entire anterior upper jaw region around a transverse axis at the supraoccipital-parietal junction. In the typical birds an

analogous situation exists, although the dorsal-ventral flexion occurs in the posterior nasal region, since the parietal-occipital union is firm. The extensive movements of the bones of the nasal and palato-maxillary components seen in Elaphe are impossible owing to the fusion of the bones. The pterygo-sphenoid articulation in birds and lizards (with some notable exceptions) limits the movements of the pterygoid bone itself chiefly to the rostro-caudal directions. When the mouth is opened the pterygoid bones are adducted (rather than abducted as in Elaphe) as well as protracted, since the laterally-curving dorso-medial edge of the pterygoid bone must remain in relatively close apposition to the fixed pterygoid process of the os sphenoidale.

Adduction of the pterygoid bone during opening of the mouth likewise draws the quadrato-mandibular region mediad, thus decreasing the width of the head rather than increasing it. This has been pointed out by Bradley ('03), but bears repetition here. This feature alone would demand radical differences between the ophidian and saurian swallowing mechanisms.

In the Platynota and lizards generally the double cranial attachment of the quadrate bone (viz. to the squamosal bone and the paraoccipital process of the exoccipital bone) limits the possibility of ventral depression of the mandible as a whole around the squamosal-parietal articulation, as well as protraction around the quadrato-squamosal articulation. Thus, as compared with the condition found in the Ophidia, the saurian gape is morphologically limited in transverse, longitudinal, and vertical directions.

Finally it may be noted that among the lizards (unlike the snakes) there is no possibility for unilateral jaw action; such a possibility is ef-

fectively prevented by the double cranial attachment of the quadrate bones, the intermandibular fusion at the mental symphasis, and the fused condition of the bones of the nasal region and palato-maxillary arch. Thus in lizards there is not even the two-phase deglutitional cycle found in the snakes, but rather a simple opening-closing action of the jaws as a whole.

Hence the outline data presented in the earlier parts of Section Two ought not to be comparatively analyzed in relation to the totality of jaw function. Rather the material ought to be viewed as a summary of those saurian cranial features that preadapt the ophidian skull for the complex cranial kinesis discussed in detail previously.

CHAPTER VI

SUMMARY

1. The present investigation has been directed to a two-fold end: the determination of the functional morphology of deglutition in a generalized colubrid snake, and an analysis of the phylogenetic significance of such information. The functional approach has helped clarify and coordinate the numerous items of data on ophidian cranial osteology and myology existing in the literature, and in addition has presented for the first time an analysis of the cranial ligaments and their significance in the highly-developed kinetism and streptostylism of the ophidian skull. The present investigation has not only descriptively set forth all the bones, ligaments, and muscles involved in the deglutitional mechanism, but has correlated them and established their precise functioning during swallowing. This morphological data, analysed from the functional standpoint, has then been re-examined and correlated with the existing data on the deglutitional anatomy of the platynotan-ophidian line of reptiles, and the preadaptations and phylogenetic changes of the platynotan lizard jaw structure compared with the definitive pattern found in the advanced snakes.

2. The pertinent literature on the head region of snakes and lizards has been critically examined. Because of the wide variation in terminology used in descriptions of the cranial musculature, at was found necessary to prepare a new synonymy.

3. For the purposes of the present investigation a generalized recent colubrid snake was used, viz. a member of the rat-snake genus Elaphe. This genus was selected as being a typical representative of the numerous non-specialized Colubridae, and one most likely to show the basic morphology of the colubrids as a group. Other generalized colubrids, including Natrix, were studied for comparative purposes, and osteological material from many lizards and snakes was analyzed.

Six major modes of investigation were employed during the course of the investigation. These include observations on the swallowing process in live snakes, dissection of the head region, electrical stimulation studies on the actions of various cranial muscles and muscle groups, analyses of the tooth pattern found on prey recovered from the stomach, and cinefluorographic investigations into the movements of the cranial bones during the swallowing process. Attempts to obtain simultaneous motion picture recordings of the lateral, ventral, and dorsal aspects of the head region during swallowing were unsuccessful. The data obtained from these methods were analyzed and correlated in order to obtain a composite picture of the functional anatomy involved in swallowing.

4. The osteology and arthrology of the head region was thoroughly analyzed, and the functional components of the ophidian skull established. The numerous cranial ligaments which control the high-developed kinetics of the snake skull are presented in detail.

5. The muscles involved in deglutition have been set forth at some length; attachments, fiber direction, innervation, and relationships of those muscles of the head and neck region which are involved in the swallowing process are described.

6. The actions of these muscles and the movements of the cranial bones to which they are attached, as modified and controlled by the cranial ligaments, were then correlated in order to obtain a picture of the actual functioning of the jaws during deglutition. An analysis of the axes of rotation and the planes of movement, together with the time sequences involved, was found to be a necessary part of this study and accordingly carried out. The overall deglutitional pattern was found to be a two-phase bilateral cycle in Elaphe. The basic features include an "opening" and a subsequent "closing" of the mouth on one side of the head, with alternate "closing" and "opening" of the mouth on the contralateral side. Analysis of each of the dentiferous bones has established the sequence and direction of movement, as well as the forces which direct their actions. It was found that lateral and medial rotation around the longitudinal axis of these bones plays a more important part in deglutition than has been hitherto suspected. In addition, an analysis of protraction-retraction, elevation-depression, and abduction-adduction as they occur in reference to each of the bones has been set forth at length. The data obtained was then correlated in order to establish the complete picture of ophidian jaw action during the swallowing process.

Of special significance is the analysis of the ophidian intramandibular articulation, the controlled movements of the nasal complex, and the actions and significance of the movements of the palato-maxillary component in relation to the palato-pterygoid saddle joint.

In considering all the varied movements of the dentiferous bones, the primary (and secondary, when present) forces were determined and their

effects analyzed both on the basis of individual actions and on the contributive factors each affords to the deglutitional process as a whole.

7. In order to establish the phylogenetic development of the deglutitional morphology as found in snakes, an investigation was made into the cranial osteology of several representatives of the platynotan lizards, which are commonly thought to represent the stock from which the snakes have evolved. The skulls of a primitive platynotan lizard (Heloderma), a more advanced platynotan notard (Varanus), the lizard thought to be nearest to the basal stock of the snakes (Lanthanotus), and a generalized primitive snake (Python) were compared in detail with the generalized recent snake Elaphe. Special emphasis was placed on the skeletal modifications and the development of kinetism and streptostylism found in these forms. The nasal, brain case, pterygoid, and mandibular regions, as well as the dentition, were analyzed in turn and comparisons made. By this means the cranial features of the platynotan skulls were studied from the standpoint of those characteristics which preadapt them to the modifications found in the mesokinetic and highly-streptostylic skulls of the advanced snakes. Moreover, the actual phylogenetic trends shown in an analysis of these five selected forms were traced in detail.

8. The contributions of the present investigation may be summarized as follows. For the first time a complete correlation of the osteology, myology, and arthrology of a single representative ophidian form has been presented. This data has been analyzed from the functional standpoint, a hitherto unused approached in the study of snakes. With the unifying aid of these functional studies, the extensive body of descriptive data now in the litera-

ture may be more profitably correlated, and future investigation more efficiently directed. In addition, the functional data here presented has helped to clarify the interrelationships of the snakes as a group, and of the platynotan lizards from which they are most probably derived. It has thus aided in establishing the phylogeny of the Sauria and Ophidia on a more firm basis than has hitherto been possible.

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APPENDICES

Appendix A

The Terminology of the Cranial Muscles

Many of the problems involved in homologising muscles can be traced to the use of terminology. D. Dwight Davis ('36) has succinctly pointed out some of the difficulties as regards the nomenclature of reptilian musculature. The early method of naming the muscles from their shape (e.g., trapezius, deltoideus) is now seldom practiced. Fürbringer's (1870) method of naming muscles of the vertebrates on the basis of their osseous attachment is still in vogue in some quarters, though in Chapter IV it was pointed out why the usage is unfortunate. The naming of muscles on the basis of function is still a common practice. Indeed, when one considers how many of the muscles have been named in this way the impression is had that the function is reasonably well known. Actually this is not at all the case in many instances, and often enough the supposed function turns out on investigation to be other than the real function. Muscles that are evidently homologous may perform different functions in different animals. Another factor, seldom given consideration, is that a given muscle may perform more than one function; a name based on only one of these functions may lead to an erroneous impression that this is the only function it performs.

However, until some unanimity of opinion is reached, the difficulty will continue to exist and tables of synonymy will have to be employed by each worker in myology. The present investigator has elected to retain the old

terminology rather than add to the already over-wieldy synonymy, but in doing so names are employed that are admittedly poor choices when applied to the snakes.

There follows a reference list of the muscles discussed in the present paper.

* * *

I Trigeminal Musculature

A. Adductores Mandibulae

M. adductor mandibulae externus
pars anterior
pars media
pars posterior
M. adductor mandibulae medius
pars superficialis
pars profunda
M. adductor mandibulae internus
pars anterior
pars posterior
M. adductor mandibulae profundus

B. Constrictores Dorsales

M. protractor ossis quadrati
M. protractor ossis pterygoidei
M. levator ossis pterygoidei
M. retractor ossis pterygoidei
M. retractor vomeris

C. Constrictores Ventrales

M. intermandibularis anterior
pars cutaneo-mandibularis
pars glandulo-mandibularis
M. transversus branchialis
pars mucosalis
pars glandularis
M. intermandibularis posterior
pars anterior
pars posterior

II Hyoid Musculature

M. occipito-quadrato-mandibularis
M. cervico-mandibularis
M. constrictor colli

III Hypobranchial-spinal Musculature

A. Glosso-tracheal Group

M. hyoglossus
M. hyotrachealis
M. genioglossus
M. geniotrachealis

B. Cervical Group

M. costocutaneus superior
M. costocutaneus inferior
M. cervico-quadratus
M. neuro-costo-mandibularis
pars vertebralis
pars costalis
pars hyoidea
M. transversus abdominis
M. obliquus abdominis internus

IV Cranio-vertebral Musculature

M. spinalis
M. semispinalis
M. retractor costae biceps
M. transversohypapophyseus
pars dorsalis
pars ventralis
pars lateralis

Appendix B

Table of Muscle Synonymy

M. Adductor Mandibulae Externus

Pars anterior: Cowan & Hick

Capiti mandibularis superficialis: Adams
Masseter: Owen, McKay, Rosen (part), Hager, Radovanović
Temporalis: Teutleben (part), Kellicott
Temporalis anterior: Duvernoy, Jones, Phisalix, Fairley, Scortecci, Edgeworth (part)
Adductor externus superficialis: Lakjer, Hass, Lubosch
Post-orbito-maxillaris: Duges
Parieto-quadrato-mandibularis: Hoffmann (part)
Retractor anguli oris: Kesteven
Schliesser des Maules: Hübner, D'Alton (part)

Pars media: Cowan & Hick

Capiti mandibularis medius, heads 1-2: Adams
Masseter: Kesteven, Kellicott (part), Rosen (part)
Temporalis: Owen, Teubleben (part)
Temporalis, part 1: Hager, Edgeworth (part)
Temporo-maxillaris: Duges (part)
Parieto-quadrato-mandibularis: Hoffmann (part)
Adductor externus medialis: Lakjer, Hass, Lubosch
Schliesser des Maule: D'Alton (part)
Temporalis medialis: Duvernoy, Jones, Fairley
Temporalis anterior: McKay
Hebemuskel der Mandibel: Stannius (part)

Pars posterior: Cowan & Hick

Capiti mandibularis medius, head 3: Adams
Masseter Kellicott (part), Rosen (part)
Temporalis: Edgeworth, Kesteven (part)
Temporalis posterior: Jones, Teutleben, McKay, Fairley
In Part: Duvernoy, Owen, Phisalix, Radovanović, Scortecci
Temporalis, part 3: Hager
Temporo-maxillaris: Duges (part)
Parieto-quadrato-mandibularis: Hoffmann (part)
Schliesser des Maule: D'Alton (part)
Hebemuskel der Mandibel: Stannius (part)
Adductor externus profundus: Lakjer, Hass, Lubosch

M. Adductor Mandibulae Medius, partes superficialis et profundus:
Cowan & Hick

Capiti mandibularis medius, head 3: Adams
Temporalis: Hager (part), Edgeworth (part), Kesteven (part)
Temporalis posterior; in part: D'Alton, Duvernoy, Jones, Owen, Phisalix, Fairley, Radovanović, Scortecci
Parieto-quadrato-mandibularis: Hoffmann (part)
Tempore-maxillaris: Duges (part)
Schliesser des Maul: D'Alton (part)
Pterygoideus externus: McKay
Adductor mandibulae posterior: Lakjer, Haas
Kebemuskel der Mandibel: Stannius (part)
Masseter: Kellicott (part), Rosen (part)

M. Adductor Mandibulae Internus

Pars anterior: Cowan & Hick

Pterygoideus: Lakjer, Haas, Edgeworth (part), Radovanović (part)
Pterygoideus externus: Duvernoy, Jones, Stannius, Teutleben (part), Kellicott, Phisalix, Fairley, Scortecci
Pterygoideus internus: McKay (part), Kesteven
Pterygoideus anterior: Adams
Ectopterygoideus: Owen, Kellicott
Transverso-pterygo-mandibularis: Hoffmann
Transverso-maxillo-pterygo-mandibularis: Rosen (part), Hager
Maxillo-pterygoideus: Duges
Aeusser Flugelmuskel: D'Alton

Pars posterior: Cowan & Hick

Pterygoideus: Edgeworth (part)
Pterygoideus internus: Duvernoy, Jones, Stannius, McKay (part), Phisalix, Fairley, Scortecci
Pterygoideus posterior: Adams
Pterygo-mandibularis: Hager
Articulo-pterygoideus: Duges
Pterygoideus accessorius: Lakjer, Haas
Entopterygoideus: Owen, Kellicott
Pterygoideus externus: Teutleben (part)
Pterygoideus medius: Kesteven
Transverso-maxillo-pterygo-mandibularis: Hoffmann (part)
Aeusser Flügelmuskel: D'Alton (part)

M. Adductor Mandibulae Profundus: Cowan & Hick

Pterygoideus externus: Kesteven
Temporalis anterior: Radovanović
Pseudotemporalis: Lakjer, Hass, Lubosch
Temporalis: D'Alton (part), Hager (part), Edgeworth (part)
Parieto-mandibularis profundus: Phisalix, Scortecci
Hebemuskel der Mandibel: Stannius (part)
Masseter: Kellicott (part), Rosen (part)
Parieto-quadrato-mandibularis: Hoffmann (part)
Parieto-mandibularis: McKay

M. Protractor Ossis Quadrati: Lakjer, Hass, Lubosch, Cowan & Hick

Pterygo-sphenoidalis posterior: Hoffmann (part), Hager, Adams, Edgeworth (part), Radovanović
Pterygoideus medius: Kesteven
Pterygoideus internus: Teutleben (part)
Pterygo-sphenoidalis posterior: Hoffmann (part), Edgeworth (part)
Suboccipito-quadrato-mandibularis: Hoffmann (part), Hager, Adams
Depressor tympani: Owen
Innerer, hinterer Flügelmuskel: D'Alton (part)
Hervorzieher des Pterygoids: Stannius (part)

M. Protractor Ossis Pterygoidei: Lakjer, Hass, Lubosch, Cowan & Hick

Pterygo-sphenoidalis posterior: Hoffmann (part), Hager, Adams, Radovanović, Edgeworth (part)
Prespheno-pterygoideus: Owen
Spheno-pterygoideus: Dugas, Jones, Kellicott, Phisalix, Fairley, Scortecci
Pterygoideus internus: Stannius (part)
Pterygo-quadratus: Kesteven
Pterygo-sphenoidalis: McKay
Innerer, hinterer Flügelmuskel: D'Alton (part)
Hervorzieher des Pterygoids: Stannius (part)

M. Levator Ossis Pterygoidei: Lakjer, Hass, Lubosch, Cowan & Hick

Pterygo-sphenoidalis anterior: Radovanovic, Adams
Spheno-pterygoideus: Kesteven
Parieto-pterygoideus: Fairley
Postorbito-pterygoidien: Dugas, Scortecci
Postorbito-palatine: Duvernoy, Jones
Pterygoideus internus: Teutleben (part), Kellicott (part)
Pterygo-parietalis: Hoffmann, Hager, Edgeworth
Hebemuskel der inneren Flügelbeins: D'Alton
Heber des Pterygoids: Stannius

M. Retractor Ossis Pterygoidei: Lakjer, Haas, Lubosch, Cowan & Hick
Pterygo-sphenoidalis anterior: Hoffmann, Hager, Adams, Edgeworth, Radovanović
Spheno-pterygoideus anterior: Kesteven
Prespheno-palatine: Owen
Spheno-palatinus: Duges, Duvernoy, Jones, Kellicott, Phisalix, Fairley, Scortecci
Innerer vorderer Flügelmuskel: D'Alton
Parieto-palatinus: McKay

M. Retractor Vomeris: Stannius, Lakjer, Haas, Lubosch, Cowan & Hick
Vomero-sphenoidalis: Hoffmann, McKay, Adams, Edgeworth
Spheno-vomerinus: Duges, Duvernoy, Phisalix, Scortecci
Sphenoidalis anterior: Kesteven (part); in text
Sphenoidalis posterior: Kesteven (part); in table
Prespheno-vomerine: Jones, Owen
Pterygo-sphenoidalis anterior: Hager (part)
Zuruck zieher des Vomer: D'Alton

M. Intermandibularis Anterior

Pars cutaneo-mandibularis
Intermandibularis anterior, pars posterior: Adams, Cowan & Hick
Intermaxillaris (in part): Hoffmann, Gnanamuthu
Intermandibularis (in part): Duvernoy, McKay, Hager
Intermandibularis anterior (in part): Owen, Phisalix, Edgeworth, Scortecci
Submentalis (in part): Kellicott, Kesteven
Die sich kreuzenden Muskel des Unterkiefer (in part): D'Alton
Adductor mandibulae (in part): Duges
Mylohyoideus or anterior adductor (in part): Jones

Pars glandulo-mandibularis
Intermandibularis anterior, pars anterior: Adams, Cowan & Hick
Intermaxillaris (in part): Hoffmann, Gnanamuthu
Intermandibularis (in part): Duvernoy, McKay, Hager
Intermandibularis anterior (in part): Owen, Phisalix, Lubosch, Edgeworth, Scortecci
Submentalis (in part): Kellicott, Kesteven
Die sich kreuzen den Muskeln des Unterkiefers (in part): D'Alton
Mylohyoideus or anterior adductor (in part): Jones

M. Transversus Branchialis

Pars mucosalis

Transversus branchialis: Cowan & Hick
Intermandibularis ("a more dorsal part"): Edgeworth (?)
Genioglossus, lateral division: Gnanamuthu
Intermandibularis, pars dorsalis: Lubosch

Pars glandularis

Not previously distinguished

M. Intermandibularis Posterior

Pars anterior: Cowan & Hick
Intermaxillaris: Gnanamuthu (part)
Intermandibularis posterior: Owen, Phisalix, Edgeworth, Scortecci
Adductor mandibularis: Duges (part)
Adductor medius: Adams
Laryngo-maxillaris: Kellicott
Intermandibularis: McKay (part)
Mylohyoideus or anterior adductor: Jones (part)
Intermandibularis, pars longitudinalis: Lubosch

Pars posterior: Cowan & Hick
Intermandibularis: Kesteven
Intermandibularis posterior: Edgeworth
Adductor posterior: Jones, Adams
Submaxillaris: Kellicott (part)
Die sich kreuzenden Muskeln des Unterkiefers: D'Alton

M. Occipito-quadrato-mandibularis: Hoffmann, Adams, Edgeworth, Cowan & Hick

Digastricus: Duvernoy, Jones, McKay, Phisalix, Fairbey, Scortecci
Depressor mandibulae, pars cephalognathus: Kesteven
Quadrato-mandibularis: Kellicott
Tympanico-mandibularis: Owen
Post-tympanico-mandibularis: Duges
Niederzieher des Unterkiefers: D'Alton
Temporalis: Teutleben (part), Rosen (part)

M. Cervico-mandibularis: Hoffmann, Rosen, Lubosch, Edgeworth, Cowan & Hick

Retractor oris: McKay
Trachelo-mastoideus: Owen, Kellicott
Nackenunterkiefermuskel: D'Alton
Temporalis: Teutleben (part)
Depressor mandibulae: Adams

M. Constrictor Colli: Duvernoy, Edgeworth, Kesteven, Cowan & Hick
Platysma: McKay
Atlanto-epistropheo-hyoideus: Hoffmann
Rückwärtszieher des Zungenbeins: D'Alton
Facialis-constrictor: Lubosch

M. Hyoglossus: Owen, Hoffmann, McKay, Kellicott, Adams, Edgeworth, Cowan & Hick
Zungenbeinmuskel: D'Alton
Hyo-vaginiens: Jones

M. Hyotrachealis: Kellicott, Lubosch, Edgeworth
Hyolaryngeus: Cowan & Hick
Retractor laryngeus: Göppert
Hyoglossus: Kesteven (?)
Rückwärtszieher des Kehlkopfs: D'Alton

M. Genioglossus: Owen, Kellicott, Adams, Edgeworth, Kesteven, Cowan & Hick
Genioglossus, dorsal division: Gnanamuthu
Genio-hyoideus or maxillo-hyoideus: Hoffmann
Genio-hyoglossus: McKay
Genio-vagiens: Duvernoy, Jones
Vorwärtszieher des Zungenbeins: D'Alton

M. Geniotrachealis: Jones, Owen, Kellicott, Edgeworth, Cowan & Hick
Genioglossus, ventral division: Gnanamuthu
Protractor laryngeus: Göppert
Maxillo-laryngeus: Hoffmann, Adams
Vorwärtszieher des Kehlkopfes: D'Alton

M. Costocutaneus superior: Buffa, Mossauer
Cutaneous externus: Hoffmann
Obliquus externus: McKay
Der grosse äussere oder Seitenhautmuskel: D'Alton

M. Costocutaneus inferior: Buffa, Mossauer
Cutaneous internus: Hoffmann
Obliquus internus: McKay
Der innere oder untere Bauchhautmuskel: D'Alton

M. Cervico-quadratus: Edgeworth, Cowan & Hick
Retractor ossis quadrati: Hoffmann, McKay, Adams, Lubosch, Radovanović, Kesteven
Cervico-squamosal: Phisalix
Submaxillo-quadratus: Kellicott
Rückwärtszieher des quadratum: D'Alton

M. Neuro-costo-mandibularis

Pars vertebralis: Cowan & Hick

Neuro-mandibularis: Duvernoy, Owen, Kellicott, Hager, Phisalix, Adams, Lubosch, Radovanović, Scortecci
Neuro-costo-mandibularis: Edgeworth (part)
Cervico-maxillaris: Duges
Cervico-hyomandibularis lateralis: Kesteven
Depressor mandibulae: McKay (part)
Cervico-hyoideus: Hoffmann (part)
Nackenzungenbeinmuskel: D'Alton
Vertebro-mandibularis: Jones, Fairley

Pars costalis: Cowan & Hick

Costomandibularis: Duvernoy, Jones, Owen, McKay, Hager, Phisalix, Adams, Fairely, Radovanović, Scortecci
Costo-maxillaris: Duges
Sternohyoideus et hyomandibularis superficialis: Kesteven
Neuro-costo-mandibularis: Edgeworth (part)
Cervico-hyoideus: Hoffmann (part)
Rectus system: Lubosch

Pars hyoidea: Cowan & Hick

Mylohyoideus: Owen, Hoffmann, McKay, Phisalix, Adams, Scortecci
Kiefernzungenbeinmuskel: D'Alton
Latissimus ingluviei, s. platysma myoides: Hübner
Submaxillaris: Kellicott (part)
Geniohyoid: Edgeworth
Branchiomandibularis spinalis: Lubosch

M. Transversus abdominis: Mosauer

Abdominis internus: Hoffmann
Transversalis: McKay (part)
Der innere Bauchmuskel: D'Alton

M. Obliquus Abdominis internus: Mosauer

Abdominis externus: Hoffmann
Transversalis: McKay (part)
Der äussere Bauchmuskel: D'Alton

M. Spinalis: McKay

Semispinalis et spinalis: Mosauer (part), Nishi (part)
Capitovertebralis: Hoffmann (part)
Der aufsteigende Muskel zwischen den Dorn- und Gelenkfortsatzen: D'Alton (part)

M. Semispinalis: McKay
Semispinalis et spinalis: Mosauer (part), Nishi (part)
Capitovertebralis: Hoffmann (part)
Der aufsteigende Muskel zwischen den Dorn- und Gelenkfortsätzen: D'Alton (part)

M. Retractor costae biceps: Hoffmann, Mosauer
Costalis s. retractor costae: McKay
Der zweibauchige Rückwärtszieher der Rippen: D'Alton

M. Transversohyperapophyseus: Mosauer
Subvertebralis rectus: McKay

Appendix C

List of Specimens Used

Legend:

CNHM - Chicago Natural History Museum
LPZ - Lincoln Park Zoo, Chicago
RZ - Rochester Zoo, New York
EMN - Dr. Edward M. Nelson, Loyola University, Chicago
FLO - Commercial Source, Silver Springs, Florida

Specimen	Source	Number of Specimens
Elaphe vulpina	CNHM - 43600, 41851, 46038, 2675	4
Elaphe guttata	CNHM - 8100, 4281, LPZ - (2)	4
Elaphe laeta	CNHM - 28563, 21635, 6179, LPZ - (1)	4
Elaphe obsoleta obsoleta	CNHM - 31782, 31957, 35260, and unaccession	4
Elaphe obsoleta quadrivittata	LPZ - (1) FLO - (22)	23
Natrix cyclopion floridana	CNHM - unaccession	7
Natrix sipedon pictiventris	CNHM - unaccession	6
Lampropeltis getulus floridana	CNHM - unaccession	1
Thamnophis sirtalis sirtalis	CNHM - unaccession	5
Drymarchon corais couperi	CNHM - unaccession	1
Coluber constrictor priapus	CNHM - unaccession	1
Coluber constrictor flaviventris	EMN	1
Heterodon contortrix contortrix	FLO	4
Crotalus atrox	RZ (*)	3
		68

(*) Courtesy of Marlin Perkins, Lincoln Park Zoo, Chicago, and Edward M. Nelson, Loyola University, Chicago

Appendix D

Analysis of Tooth Pattern

Details of the method used in obtaining the tooth pattern record shown on the following page are included in Chapter III. The blue (hectograph) dots were recorded directly from the tissue paper tracings, which in turn were taken directly from the ingested material. The blue writing, lines, etc. are a part of the permanent record; the black lines, etc. are included here merely as an aid to interpreting the recording.

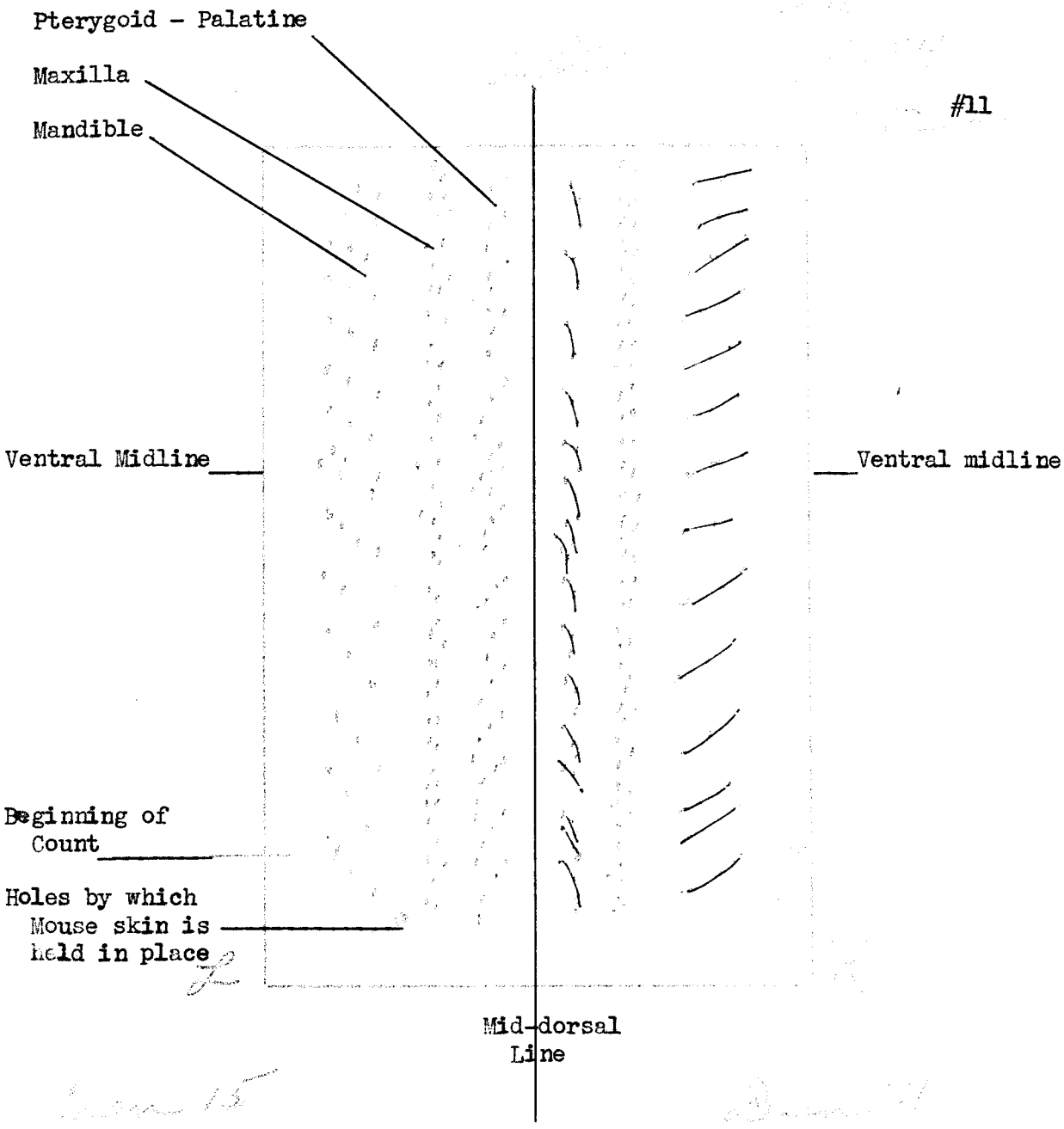
The numbers at the bottom of the record indicate the number of times the dentary and maxilla on each side were moved forward over the "recording area". The beginning of this area was indicated by a mark made on the frankfurter before feeding; the count was begun when the anterior end of the dentary or maxilla passed beyond the end of the frankfurter. These counts were found to be helpful in interpreting the dots on the permanent record.

On the right side of the record the dots have been connected to indicate the position of the dentary, palatine, and pterygoid bones during various stages of the swallowing process. The maxilla remains in the same longitudinal plane; hence the various positions of this bone overlap, and no information(other than its general position) can be determined by this technique. The posterior pterygoid teeth are too short to leave any noticable impression; this fact aids in interpretation of the record, since overlapping of the marks is held to a minimum. The palatine and anterior pterygoid teeth make deeper

impressions (shown here), and the area of the pterygo-palatine articulation is shown to advantage.

Only every third or fourth visible tooth mark is included on the final copy in order to simplify analysis. The dots shown in the final copy are a good deal larger than the actual holes made by the teeth in the casing of the frankfurter.

(Specimen Page)



Appendix E

Cinefluorograph Tracings

On the following pages are examples of the outline drawings taken directly from the cinefluorographic film used in this investigation. With this technique many details are lost; e.g., the teeth do not show for the most part. This is due in part to the lack of sharp differentiation inherent in cinefluorographs, and to the fact that the equipment available at Rochester was not designed for such relatively small material

The 16mm film, from which the drawings were made, was projected onto a translucent plastic screen on which the grid lines had previously been drawn. The outline of the projected picture was quickly sketched directly on the back surface of the screen. To prevent burning, the film was exposed to the heat of the projection lamp for only ten or twelve seconds at a time. The drawing was then transferred from the screen to tracing paper, reversed (in order to have the specimens facing to the right, as in the Plates), and then re-traced onto a permanent record. The grid lines on the screen, tracing paper, and final copy were made to correspond, thus aiding comparative analysis.

As is apparent, only some of the features pictured on a film frame were able to be included in a single drawing.

Figure A

Lateral aspect of the head region showing the "opening" phase on the right side of the mouth. Note that at this time the right maxilla is elevated, and the region of the palato-pterygoid articulation depressed. The left squamosal-quadrate-mandibular complex is also shown here; the left palato-maxillary arch is visible in the cinefluorograph, but to include it here would only cause confusion since the right palato-maxillary arch is superimposed on it for the most part. Note that the cranium and upper jaw region are elevated, as compared with Figure B. The squamosal-quadrate angle is less apparent in this figure than it is in other frames; however it is greater than 90°. Note that the squamosal bone itself angles caudo-ventrad from its parietal articulation.

Figure B

Lateral aspect of the head region showing the "closing" phase on the right side of the mouth. The left mandible has not yet been protracted. Note depression of the maxilla on the right side, and the general depression of the cranium and upper jaw as compared with Figure A. The squamosal-quadrate angle is less than 90°; the squamosal bone itself angles caudo-dorsad from its parietal articulation.

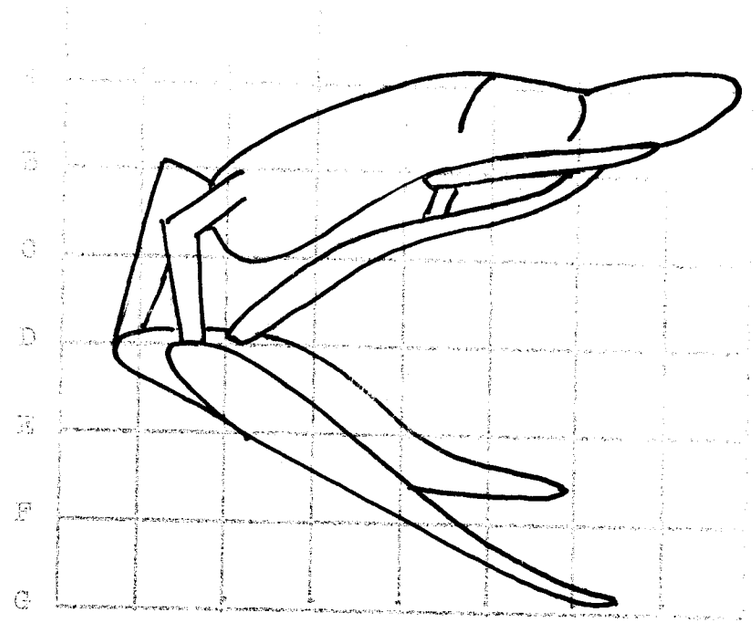


Figure A

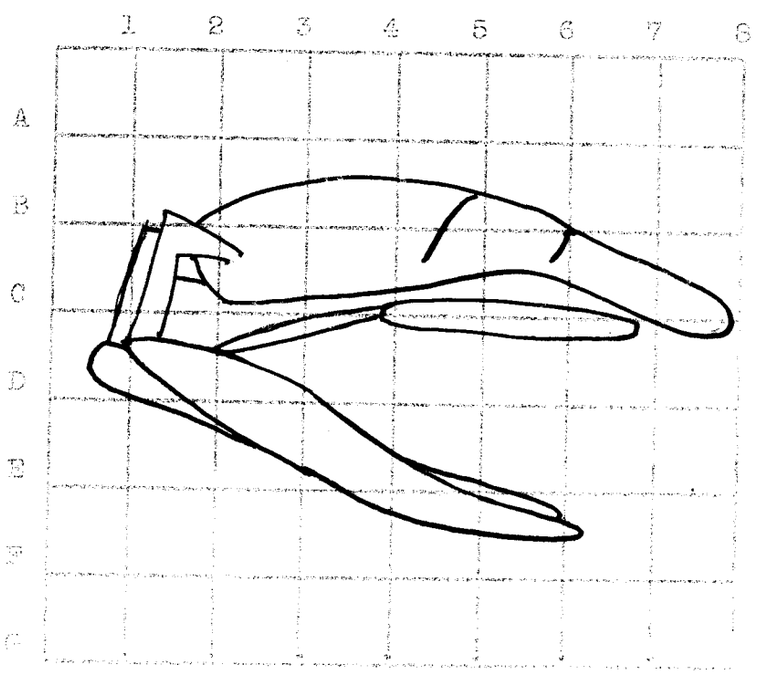


Figure B

Figure C

Lateral aspect of the head, showing structures on right side only. Mouth is just beginning to be opened.

Figure D

Lateral aspect of the head, twenty-three frames after Figure C. At this point the head is being flexed to the left; note the apparent shortening of the cranium and nasal components. From this aspect the inward flexion of the tip of the dentary bone may be seen; rotation of the dentary-splenial complex takes place around the vertical axis of the intramandibular articulation.

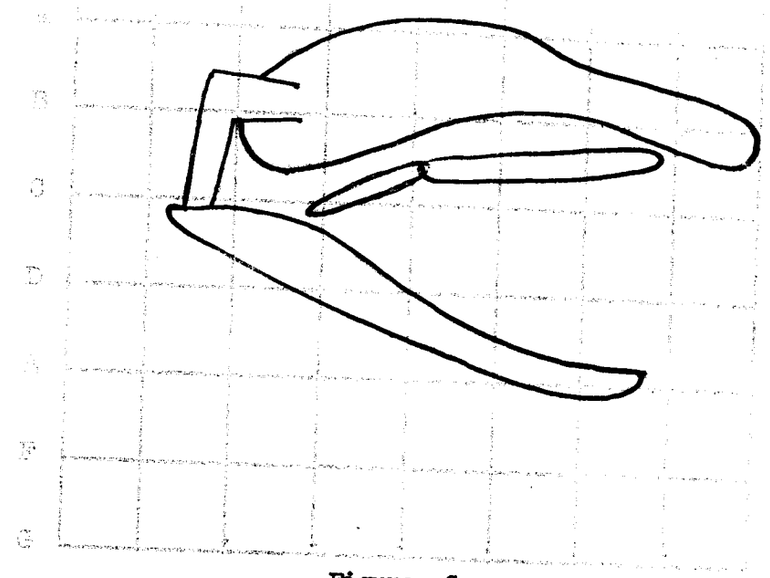


Figure C

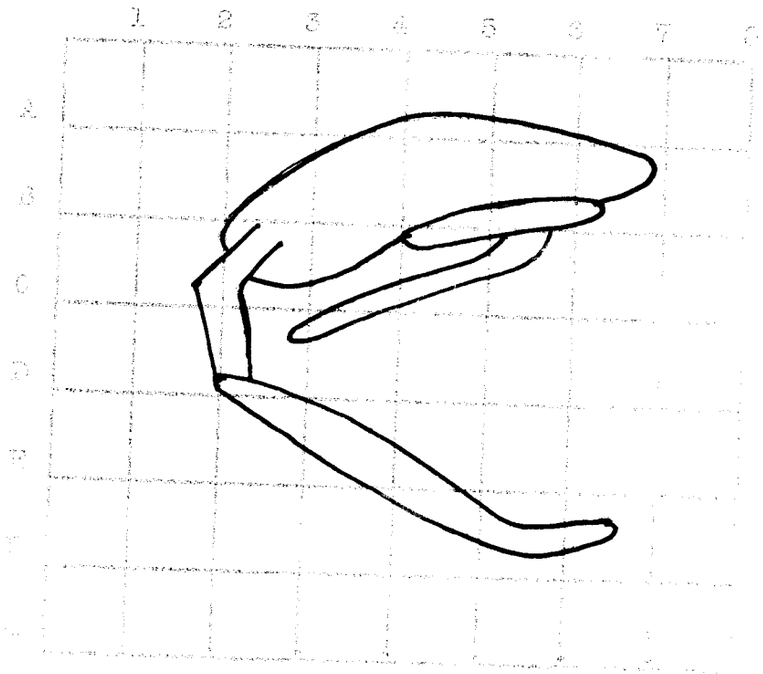


Figure D

Figure E

Lateral aspect of the head, showing relationship of the two palato-maxillary arches during opening of the right side of the mouth. Note how the right maxilla is elevated high, and the left maxilla depressed to such a degree that it appears ventral to the right pterygoid bone. It may be noted that there is no trace of flexion around the transverse axis of the left palato-pterygoid articulation, since the left side of the mouth is closed at this time.

Figure F

Lateral aspect of the head, showing degree of depression of the right maxilla when the mouth is closed. Note that the ecto-pterygoid bone extends latero-ventrad, rather than latero-dorsad as in Figure E. Depression of the cranium makes it appear as if the pterygoid bone is lateral to the otic region; actually it is near the basis hemoid mid-line, in its normal position.

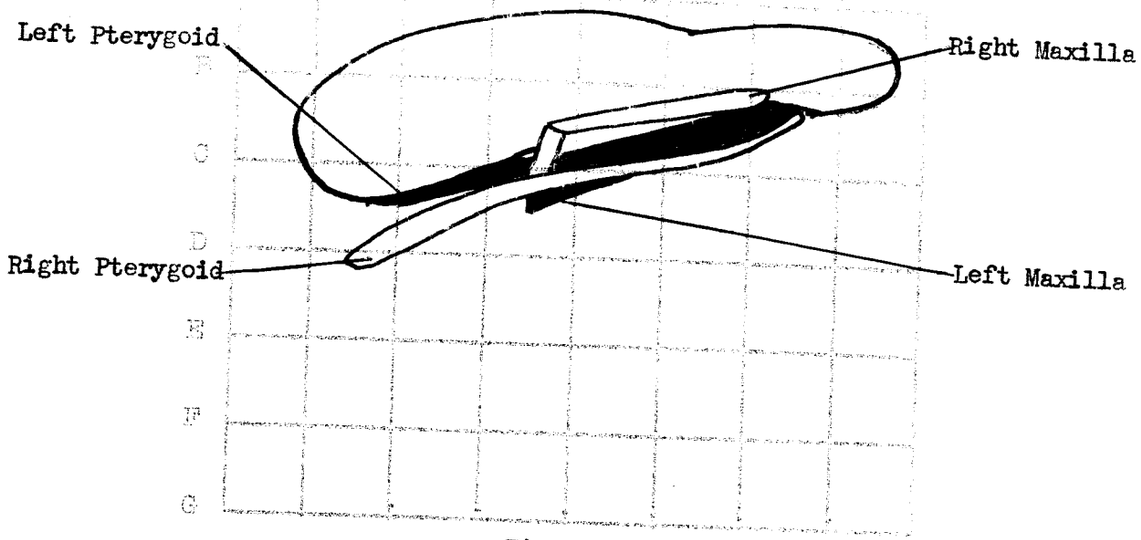


Figure E

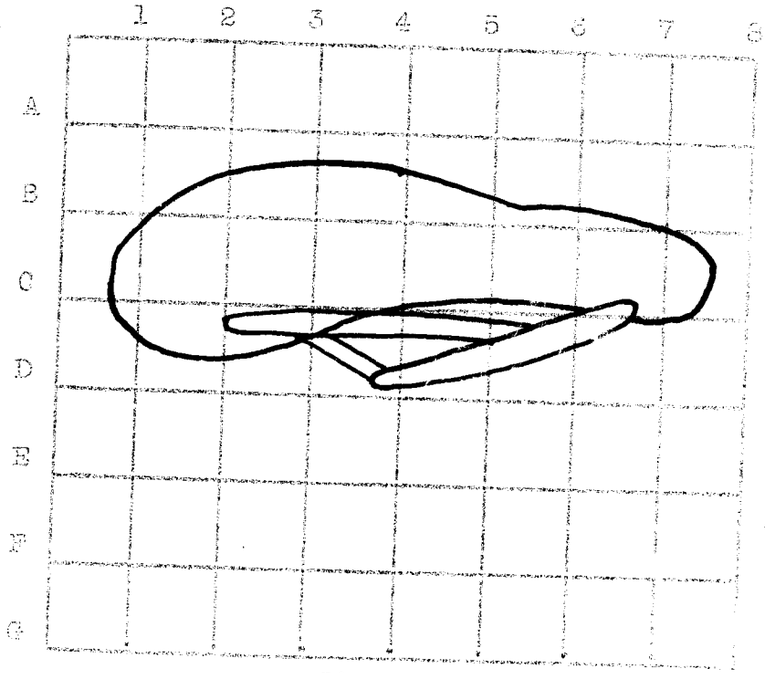


Figure F

P L A T E S

Abbreviations

AEx, 1	M. adductor mandibulae externus, pars anterior
AEx, 2	M. adductor mandibulae externus, pars media
AEx, 3	M. adductor mandibulae externus, pars posterior
AIn, 1	M. adductor mandibulae internus, pars anterior
AIn, 2	M. adductor mandibulae internus, pars posterior
AM, 1	M. adductor mandibulae medius, pars superficialis
AM, 2	M. adductor mandibulae medius, pars profunda
ANg	Os angulare
APr	M. adductor mandibulae profundus
Art	Articular facet
BaO	Os basioccipitale
BaH	Os basihyale
Car	Carotid artery
CCI	M. costocutaneus inferior
CCS	M. costocutaneus superior
CM	Centimeter
CmP	Os compositum
CnC	M. constrictor colli
Col	Columella auris
Cos	Costae
CtH	Os ceratohyale
CvM	M. cervico-mandibularis
CvQ	M. cervico-quadratus
Den	Os dentale
EcP	Os ectopterygoideum
Eso	Esophagus
ExO	Os exoccipitale
FIM	Foramen intramandibulare (of Meckel)
FJ	Foramen jugulare
FM	Foramen magnum
FO	Foramen opticum
FPro, a	Foramen prooticum, anterior
FPro, p	Foramen prooticum, posterior
Fro	Os frontale
FsM	Fossa mandibularis

GnGl	M. genioglossus
GnTr	M. geniotrachealis
Gs	Gastrosteges
HyGl	M. hyoglossus
HyTr	M. hyotrachealis
IA, 1	M. intermandibularis anterior, pars cutaneo-mandibularis
IA, 2	M. intermandibularis anterior, pars glandulo-mandibularis
IP, 1	M. intermandibularis posterior, pars anterior
IP, 2	M. intermandibularis posterior, pars posterior
ItC	M. intercartilaginosus
LEM	Ligamentum ectopterygo-maxillare
LevPt	M. levator ossis pterygoidei
LFN	Ligamentum fronto-nasale
LIM	Ligamentum intramaxillare
LMP	Ligamentum maxillo-premaxillare
LMS	Ligamentum maxillo-septomaxillare
LPFM	Ligamentum prefronto-maxillare
LPM	Ligamentum palato-maxillare
LPSM	Ligamentum postfronto-maxillare
LPtM	Ligamentum pterygo-mandibulare
LPV	Ligamentum palato-vomerale
LQM	Ligamentum quadrato-maxillare
M	Musculus
Max	Maxilla
MM	Musculi
Mm	Millimeter
Nas	Os Nasale
NCM	M. neuro-costo-mandibularis
NCM, c	M. neuro-costo-mandibularis, pars costalis
NCM, h	M. neuro-costo-mandibularis, pars hyoidea
NCM, v	M. neuro-costo-mandibularis, pars vertebralis
ObliI	M. obliquus internus
OQM	M. occipito-quadrato-mandibularis
Pal	Os palatinum
Par	Os parietale
PoF	Os postfrontale
PrF	Os prefrontale
PrM	Premaxilla (Os incisivum)
PrO	Os prooticum
PrPtg	M. protractor ossis pterygoidei
PrQud	M. protractor ossis quadrati
PtG	Os pterygoideum

Qud	Os quadratum
RCB	M. retractor costae biceps
RePtg	M. retractor ossis pterygoidei
ReVom	M. retractor vomeris
Sep	Septomaxilla
SiSpi	M. semispinalis
SlGl	Glandula sublingualis lateralis
Sph	Os sphenoidale
Spi	M. spinalis
Spl	Os spleniale
Squ	Os squamosale
SuO	Os supraoccipitale
Tr	Trachea
TVA	M. transversus abdominis
TVB	M. transversus branchialis
TVB, l	M. transversus branchialis, pars mucosalis
TVB, 2	M. transversus branchialis, pars glandularis
TVH	M. transversohypapophyseus
TVH, d	M. transversohypapophyseus, pars dorsalis
TVH, l	M. transversohypapophyseus, pars lateralis
TVH, v	M. transversohypapophyseus, pars ventralis
V	Nervus trigeminalis
V2	Nervus trigeminalis, pars maxillaris
V3	Nervus trigeminalis, pars mandibularis
V4	Nervus trigeminalis (branch to M. levator ossis pterygoidei)
VII	Nervus facialis
Vom	Vomer

All figures are of Elaphe obsoleta quadrivittata. Scale of measurement is based on medium size adult specimens.

Plate I

Fig. 1. Lateral aspect of skull. Pterygoid teeth omitted.

Fig. 2. Dorsal aspect of skull. Anterior half of mandibles omitted

Fig. 3. Ventral aspect of skull. All teeth omitted. Palatine and pterygoid bones abducted slightly to show ventral cranial structures to better advangage

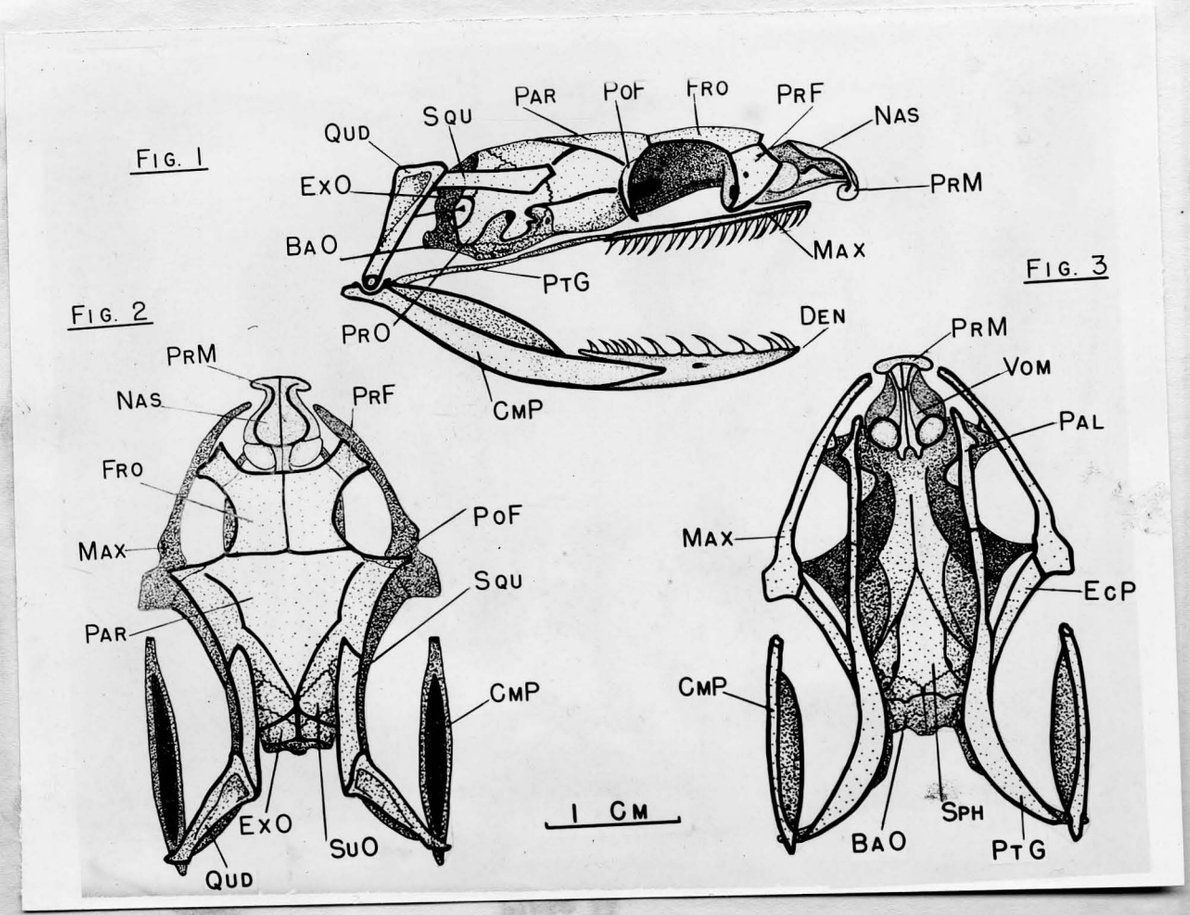


Plate II

Fig. 4. Nasal component and anterior end of cranial component of skull; lateral aspect. Prefrontal bone omitted.

Fig. 5. Anterior aspect of right half of frontal bone complex, showing articular facets. Position in cross-section of tendon of M. retractor vomeris also indicated.

Fig. 6. Posterior aspect of right half of nasal component, showing articular facets corresponding to those in Figure 5.

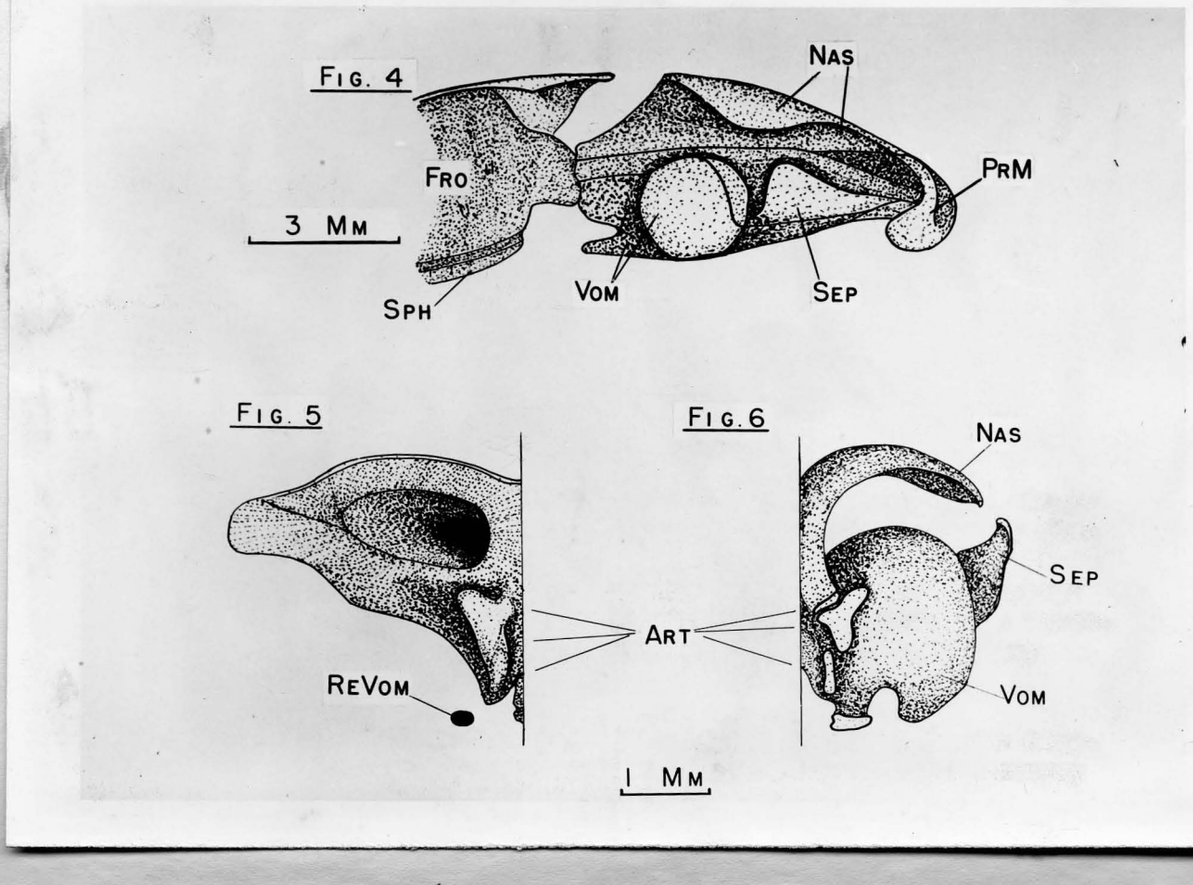


Plate III

Fig. 7. Anterior half of left mandible, medial aspect. Lettering as in Figure 8.

Fig. 8. Same as Figure 7, with bones disarticulated at the intramandibular articulation.

Fig. 9. Anterior half of right mandible, lateral aspect. Lettering as in Figure 10.

Fig. 10. Same as Figure 9, with bones disarticulated at the intramandibular articulation.

Fig. 11. Anterior aspect of the right compound-angular complex at the level of the intramandibular articulation. Lateral process of the compound bone in section.

Fig. 12. Posterior aspect of the right splenio-dentary complex at the level of the intramandibular articulation. Superior and inferior lateral processes of the dentary bone in section; position of the lateral process of the compound bone in outline.

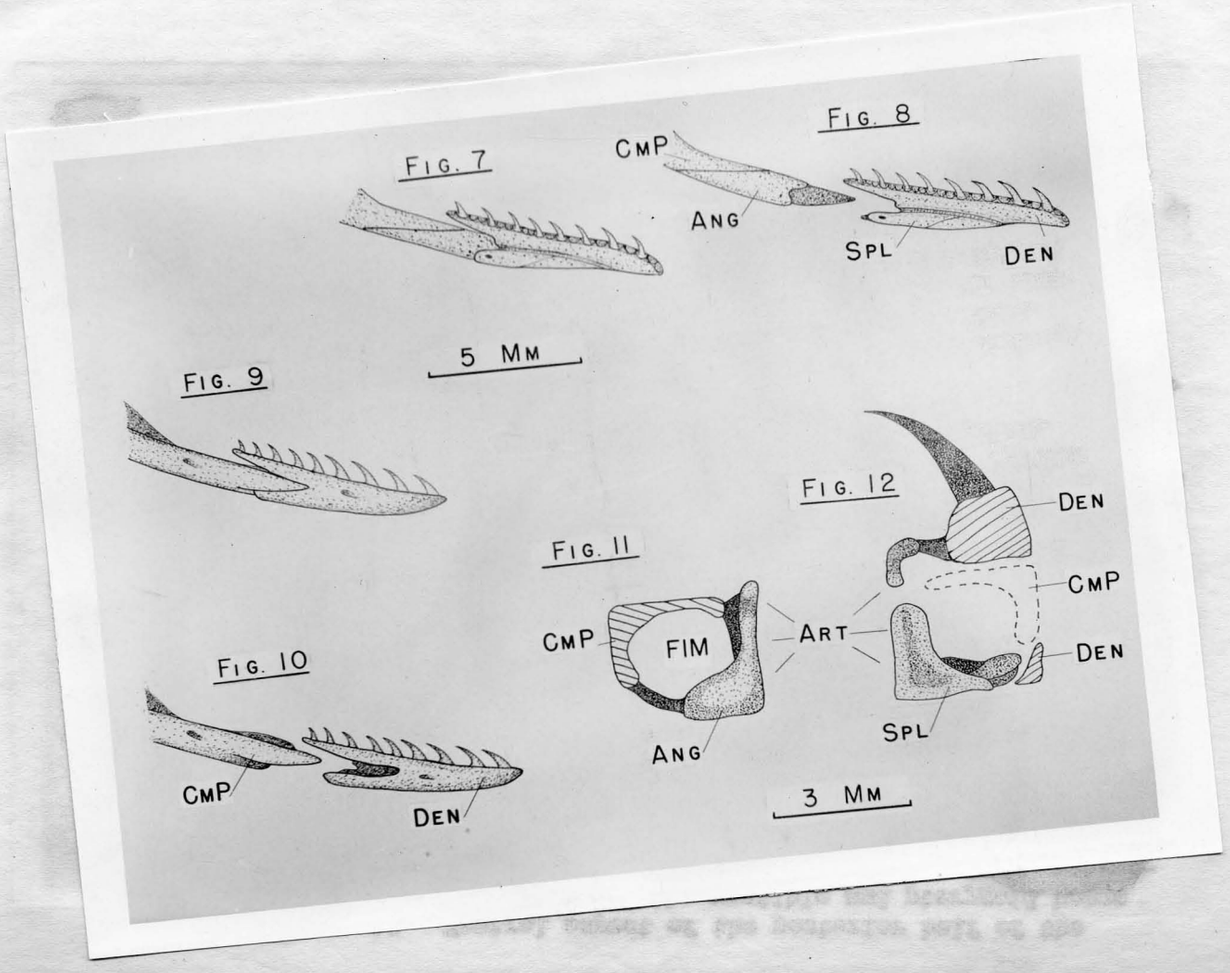


Plate IV

Fig. 13. Ventral aspect of the posterior half of the cranium; posterior halves of the mandible and pterygoid bones shown on left side only. Right side: relations of MM. retractor costae bicaps and transversohypapophyseus; insertion areas of the anterior four constrictor dorsalis muscles. Left side: MM. protractor ossis quadrati and adductor mandibulae internus, pars posterior, in situ.

Fig. 14. Posterior aspect of cranium. Right side: general topography of the region. Left side: insertion area for axial muscles; foramen for exit of the hypoglossal nerve, posterior portion, not labeled.

Fig. 15. Lateral aspect of posterior half of skull, showing insertion areas for the muscles of deglutition. The quadrate bone has been sectioned and the posterior half together with the os quadratum displaced caudad. Mandible omitted.

Fig. 16. Lateral aspect of proximal half of right mandible, showing insertion areas for the muscles of deglutition.

Fig. 17. Medial aspect of proximal half of left mandible, showing insertion areas for muscles of deglutition, and for the pterygo-mandibular ligament.

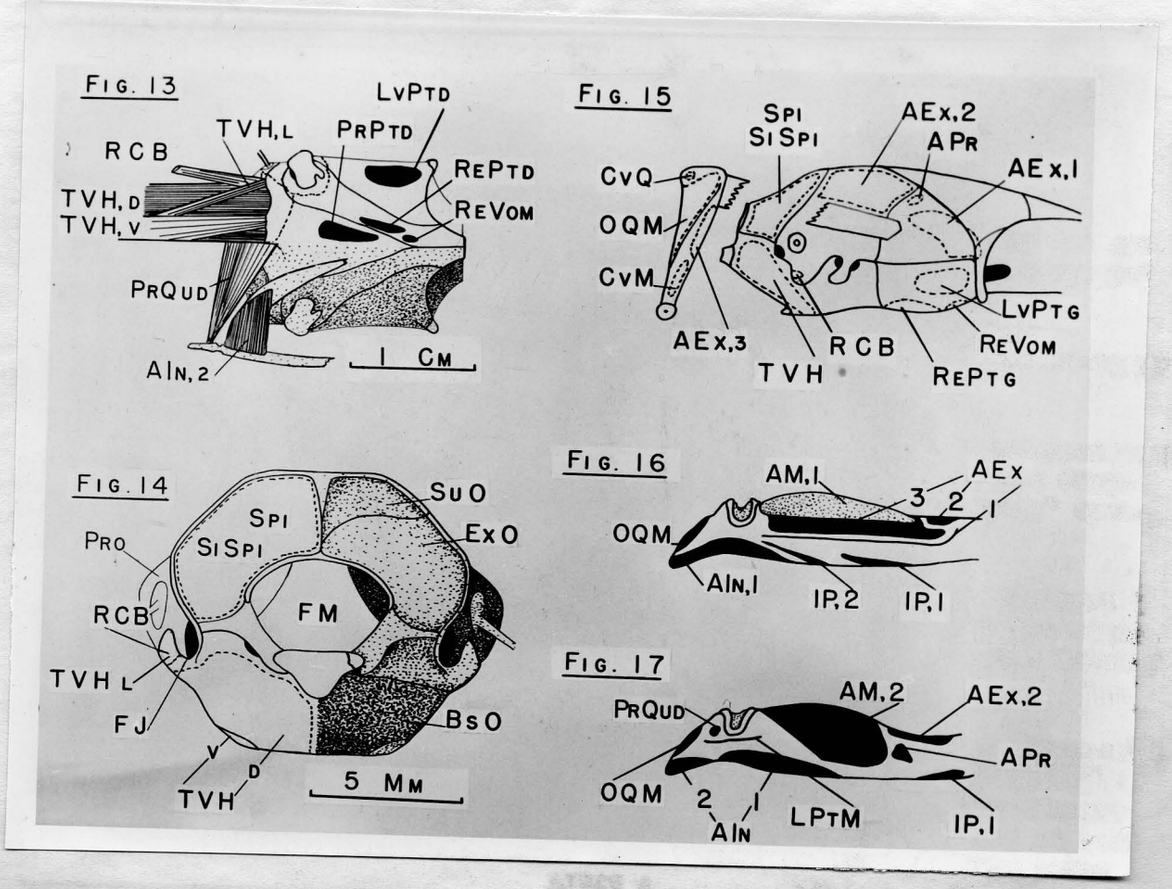


Plate V

Fig. 18. Lateral aspect of neck and posterior head region after removal of the skin; aponeurosis of M. adductor mandibulae externus, pars anterior, indicated by a straight line along its posterior border only. Prominent ligamentum quadrato-maxillare not labeled. M. constrictor colli, which is of extremely variable extent, has been shown in somewhat reduced form here.

Fig. 19. Lateral aspect of head and neck region. Same as Figure 18 after removal of the MM. constrictor colli and adductor mandibulae externus, pars posterior; pars anterior of the latter muscle transected and mandibular half removed.

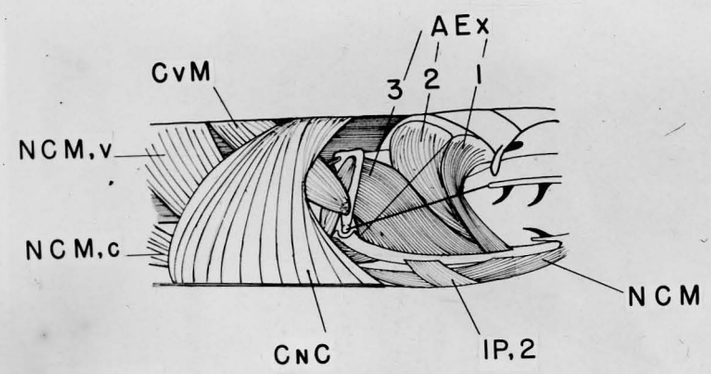


FIG. 18

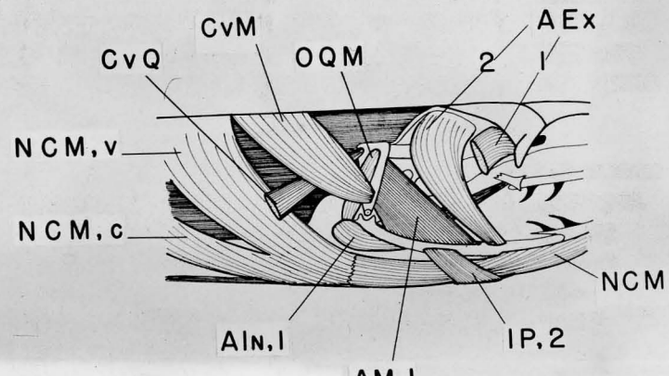


FIG. 19

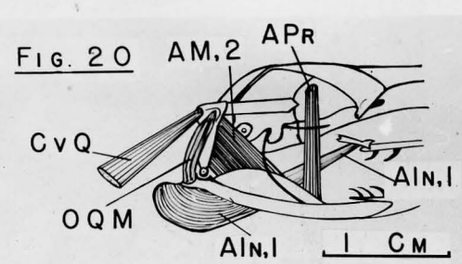
Plate VI

Fig. 20. Lateral aspect of posterior head region; axial and intramandibular musculature omitted. Same as Figure 19 after removal of MM. adductor mandibulae externus, cervico-mandibularis, and adductor mandibulae medius, pars superficialis. Maxillary and mandibular divisions of the trigeminal nerve in situ.

Fig. 21. Diagrammatic representation of trigeminal and facial nerve distribution to the muscles of deglutition; right side of head, lateral aspect. The intracranial course of the nerves is in dotted outline.

Fig. 22. Lateral aspect of right side of head showing the anterior constrictor dorsalis musculature in situ. Distal half of squamosal and ectopterygoid bones omitted. Quadrate bone and mandible, together with all the muscles that insert on them, omitted entirely. Lateral edge of palato-maxillary arch rotated ventro-mediad to a slight extent.

Fig. 23. Same as Figure 22 after removal of the M. levator ossis pterygoidei. Insertions of MM. retractor ossis pterygoidei and retractor vomeris indicated. Note position of ligamentum fronto-nasale; profrontal bone omitted.



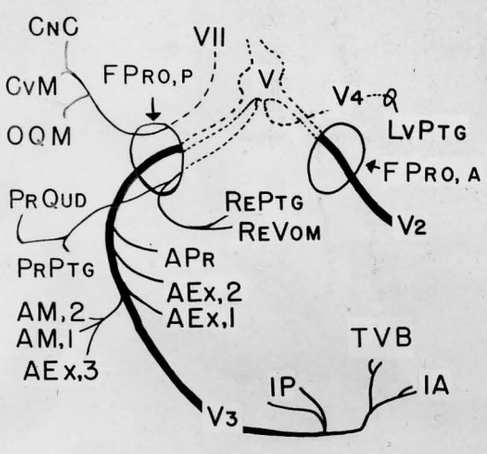
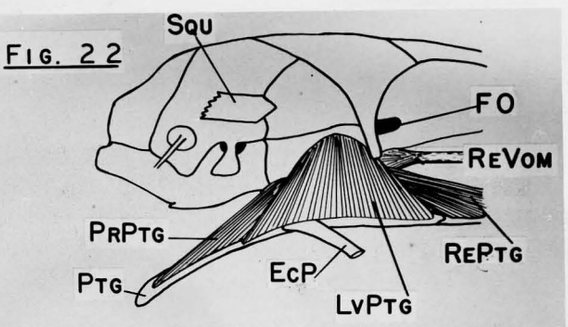


FIG. 21



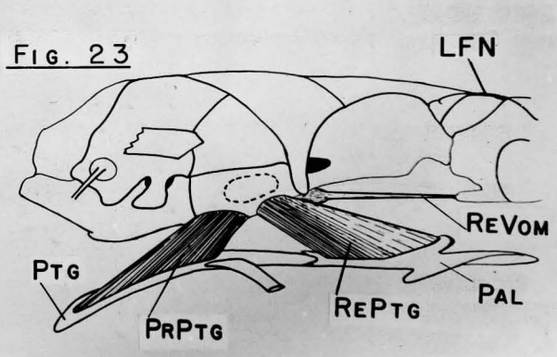


Plate VII

Fig. 24. Intermandibular musculature, dorsal aspect, after removal of the oral mucosa.
Left Side: M. transversus branchialis omitted, except for the glandular insertion. MM. intermandibularis anterior, geniotrachealis, and intermandibularis posterior, pars anterior, transected and medial portions removed.
Right Side: M. genioglossus transected and medial portion removed. Glandular slips of the MM. transversus branchialis and intermandibularis anterior each transected twice and mid-portions removed.

Fig. 25. Same as Figure 24 after removal of lingual and tracheal structures, except for origins of MM. geniotrachealis and genioglossus.
Left Side: M. intermandibularis posterior, pars anterior, transected and medial portion removed.
Right Side: Sublingual gland and attached muscles omitted entirely. M. transversus branchialis transected near mid-line and distal portion removed. M. neuro-costo-mandibularis transected twice and mid-portion removed.

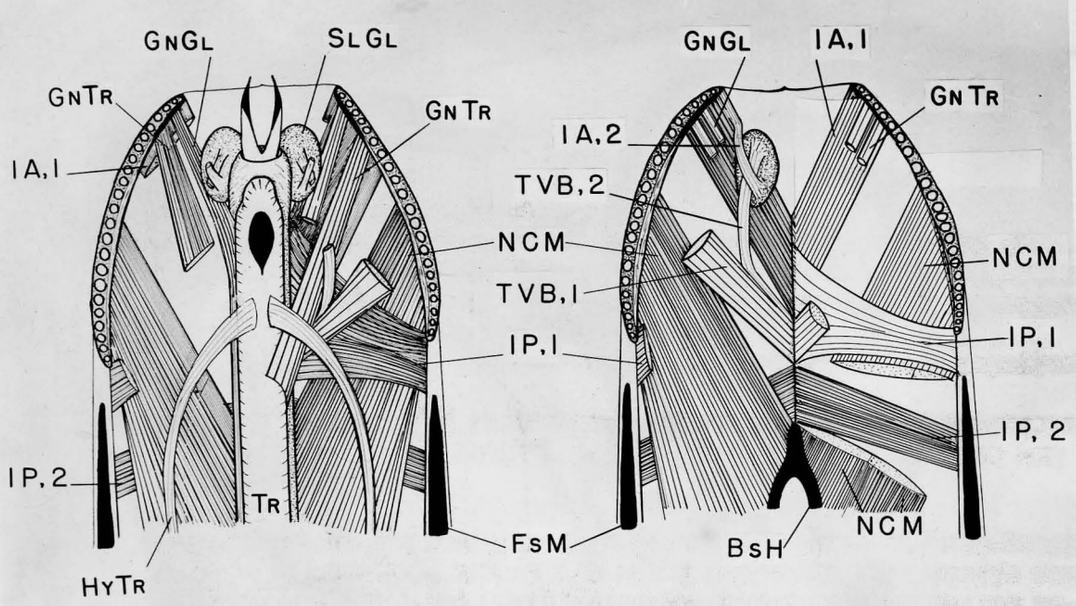


FIG. 24

FIG. 25

1 CM

Plate VIII

Fig. 26. Left half of the neck region as viewed from the right side. Cut dorsal and ventral midlines spread flat to the vertical plane of the lateral midline. Trachea, tongue, ceratohyal, esophagus, M. obliquus abdominis internus, and transversus abdominis omitted.

Fig. 27. Diagrammatic cross-section of the neck region at the level of Vertebra 6, showing relative position of the structures in the area. The esophageal mucosa normally fills in the entire space between the M. transversus abdominis and the tracheal-lingual structures.

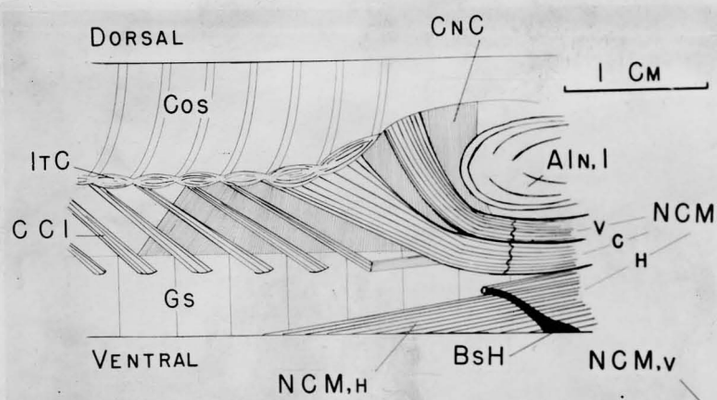


FIG. 26

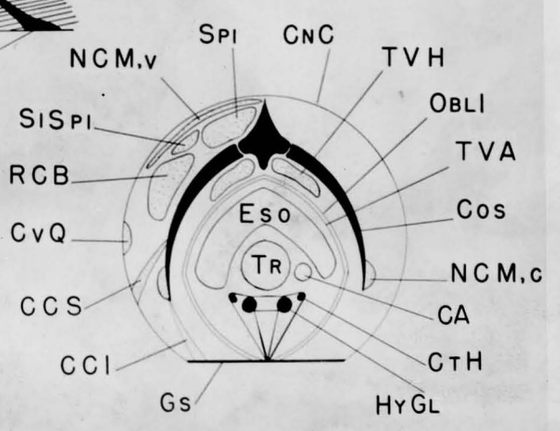


FIG. 27

Plate IX

Composite diagrammatic representations showing the direction of pull of the muscles acting on the posterior half of the mandible. The effects of the pterygoid retractor and the anterior intermandibular muscles are not shown. The directions indicated here vary somewhat during different phases of the swallowing process, and the origins and insertions of the various muscles must be recalled in analyzing the actions of the mandible and other bones of the region. Cf. text.

Fig. 28. Cross-section through the right side of the skull at a level anterior to the quadrato-mandibular articulation, as viewed from the anterior aspect. Pterygoid vane in outline; other osseous structures in section.

Fig. 29. Right lateral aspect of the posterior two-thirds of the skull.

FIG. 28

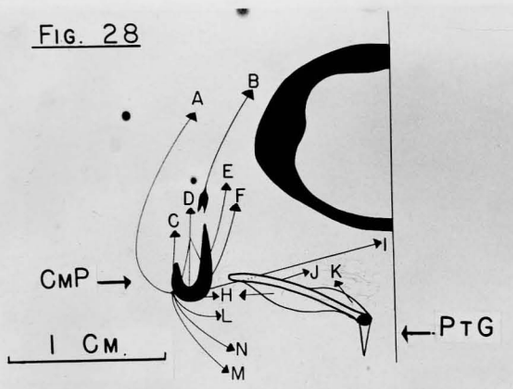
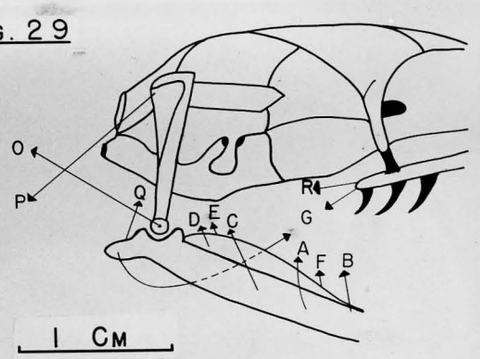


FIG. 29



MM. ADDUCTORES MANDIBULAE:

A. EXTERNUS, PARS ANTERIOR
B. " , PARS MEDIA
C. " , PARS POSTERIOR
D. MEDIUS, PARS SUPERFICIALIS
E. " , PARS PROFUNDA
F. PROFUNDUS
G. INTERNUS, PARS ANTERIOR
H. " , PARS POSTERIOR
I. M. PROTRACTOR QUADRATI
J. M. PROTRACTOR PTERYGOIDEI
K. M. LEVATOR "
M. INTERMANDIBULARIS POSTERIOR,
L. PARS ANTERIOR
M. PARS POSTERIOR
N. M. NEURO-COSTO-MANDIBULARIS
O. M. CERVICO-MANDIBULARIS
P. M. CERVICO-QUADRATUS
Q. M. OCCIPITO-QUADRATO-MANDIBULARIS
R. LIGAMENTUM QUADRATO-MAXILLARE

Plate X

Fig. 30. Diagrammatic cross-section through skull at the level of the ectopterygoid-maxillary articulation, as viewed from the anterior aspect. Ligaments and position of the maxilla and pterygoid bone during opening of the mouth (left side) and during closing (right side) are shown. Arrows indicate direction of ectopterygoid movement and position of long axis of this bone; the ectopterygoid bone itself does not appear in cross-section at this level, but the ligamentum ectopterygomaxillare is indicated to show rotational effects of the ectopterygoid bone on the maxilla. Note that in this and the following figure the caudal curvature of the pterygoid (palatine) and maxillary teeth is not apparent.

Fig. 31. Semidiagrammatic, anterior cross-sectional view of the skull at the level of the fronto-nasal articulation, showing relationship of ligaments and bones during opening of the mouth (right side) and during closing (left side). Palatine and maxillary bones shown in section.

Fig. 32. Semidiagrammatic dorsal aspect of right palato-maxillary arch and condylar region of the mandible, showing location and direction of action of the ligaments and muscles acting directly on the palato-maxillary component. Relative position of nasal component and ventral surface of the prefrontal bone indicated in outline. The prefrontal bone and the ligamentum prefronto-vomerale are not labeled.

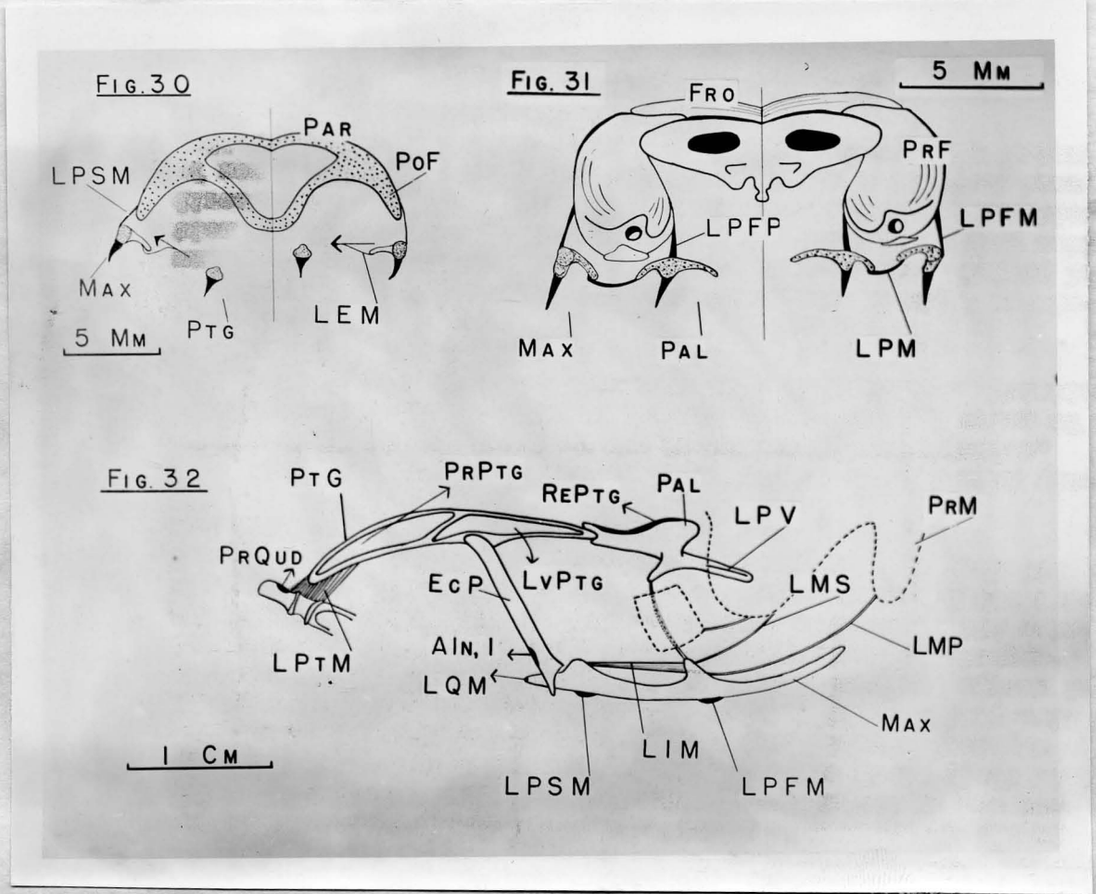


Plate XI

Figs. 33 - 34. Lateral aspect of the skull, showing variations in the interrelationships of bones during opening of the mouth (Fig. 33) and during closing (Fig. 34). Teeth and prefrontal bone omitted. Note especially the variations in the naso-cranial region, the depression of the posterior end of the squamosal bone during opening of the mouth, the rotation of the palatine and pterygoid bones around their common transverse axis, and the elevation of the maxilla during protraction-depression of the os pterygoideum. In these figures the longitudinal rotation of the mandible and palato-maxillary bones is not apparent, nor is flexion at the intramandibular articulation.

Fig. 35. Ventral aspect of the palato-maxillary arch during opening of the mouth (right side) and during closing (left side), to illustrate rotation of the palatine and pterygoid bones around the pterygo-palatine vertical axis which passes through their common articulation. Anterior ends of the maxilla and palatine bones remain at about the same respective distances from the midline of the body during opening and closing of the mouth. Elevation, depression, and longitudinal rotation of the bones are not shown in this figure; but the apparent "shortening" in length of the bones is due to elevation-depression factors. Teeth omitted.

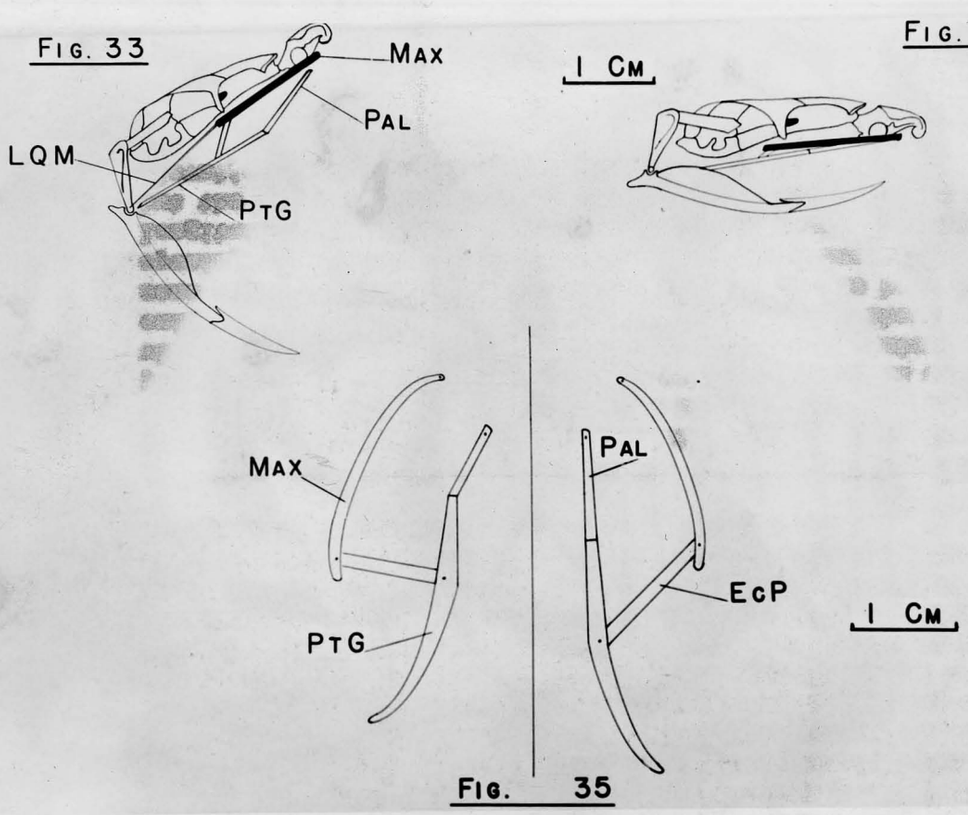


FIG. 35

APPROVAL SHEET

The dissertation submitted by Raymond Gerard Albright, S. J., has been read and approved by a committee of five members of the Graduate Faculty.

The final copies have been examined by the director of the dissertation and the signature which appears below verifies the fact that any necessary changes have been incorporated, and that the dissertation is now given final approval with reference to content, form and mechanical accuracy.

The dissertation is therefore accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

23 May 1953
Date

Edward [illegible]
Signature of Advisor